A NEUROPHYSIOLOGICAL INVESTIGATION OF THE FELINE EXTRASTRIATE VISUAL CORTEX (AREA 18) USING ORIENTED AND TEXTURED STIMULI: A COMPARISON WITH AREA 17

by

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This thesis is dedicated primarily to my parents,
and also to the memory of my Grandmother, Mrs. W.E. Priestley,
and to my Grandfather, Mr. W.E. Priestley.

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ABSTRACT

Visual noise, bar and single-spot stimuli were used to investigate areas 17 and 18 of the lightly-anaesthetized feline visual cortex.

In each area, S-cells were predominantly insensitive to motion of a field of visual noise alone. C-cells were more sensitive to noise motion than B-cells, but showed heterogeneity in noise sensitivity, which was associated with other response properties. Strongly noise-sensitive C-cells had high spontaneous activity and broad directional tuning, and were predominantly binocularly-driven and direction-selective. In area 18, as in area 17 (Hammond and Smith, 1983, 1984), deep-layer C-cells were more noise-sensitive than superficial-layer C-cells, and showed a stronger association between noise sensitivity and response properties.

In both areas 17 and 18, preferred directions for a moving bar and a field of visual noise were dissimilar. Typically, directional tuning for noise became progressively more bimodal as velocity was increased, the trough of depressed response corresponding to the peak in directional tuning for bar motion. Although tuning for bar motion was typically velocity-invariant, some cells showed variations in bar tuning with velocity, which were associated with velocity-dependent changes in noise tuning. In asymmetrically tuned cells, tuning for bar motion was broader on the flank closest to the preferred direction for noise and spot motion. Thus the relatively broad tuning for bar motion in strongly noise-sensitive C-cells probably reflects stimulation of the directional mechanism by the moving bar. In both cortical areas, C-cells had broader tuning for bar motion than S- or B-cells, but S-cells in area 18 were more broadly tuned than those in area 17.

Noise-insensitive area 18 cells, like area 17 simple cells (Hammond and MacKay, 1981b), showed suppression of responses to optimally-oriented moving bars by a background field of visual noise moving in-phase at the same velocity. Percent suppression declined non-linearly with bar length but, unlike percent end-inhibition

was velocity-invariant. Thus, the inhibitory action of synchronous background motion is probably divisive, and may derive from an axo-somatic, noise-sensitive inhibitory input predominantly via cells in neighbouring orientation 'columns'.

The results emphasize the overall similarity in neuronal organization of areas 17 and 18, and thus confirm and extend previous work; they strengthen the conclusion that the two cortical areas operate in parallel.

CHAPTER 1

PROPERTIES OF CELLS IN THE CAT RETINA AND VISUAL THALAMIC RELAY NUCLEI

PART I: RETINAL GANGLION CELLS

1.1. PHYSIOLOGICAL PROPERTIES

1.1.1. On- And Off-Centre Cells

The first description of cat retinal ganglion cell receptive fields by Kuffler (1953) has for many years formed the starting point for accounts of visual receptive fields in mammals. Retinal ganglion cells were characterized by concentric centre-surround receptive fields which were dichotomized into on- and off-centre types in order to convey temporal response characteristics to the onset or cessation of a light spot. For on-centre cells, photic stimulation of the receptive field centre evoked excitation which was followed, at light offset, by inhibition. Stimulation of the annular surround evoked inhibition which was followed, at light offset, by excitation. Maximum excitation and inhibition were obtained respectively by stimulation of the entire receptive field centre or surround. Off-centre cells had the converse receptive field organization.

It is now known that in some ganglion cells, removal of an excitatory stimulus from the receptive field leads not to inhibition, but to a rapid return to prestimulus firing rate (section 1.1.5.). In general, however, the temporal response characteristics stressed by Kuffler (1953) have been neglected in recent years and more emphasis has been placed on the capacity of on- and off-centre cells to signal respectively the presence of objects lighter or darker than the background. It has also emerged that a small minority of retinal ganglion cells do not have separate centre and surround receptive field components (section 1.1.6.), while, for a larger proportion, this is only a part of the receptive field organization (section 1.1.2.).

1.1.2. Linear (X)/Non-Linear (Y) Classification

Following Kuffler (1953) Rodieck (1965) proposed that retinal ganglion cells sum excitation and inhibition from the receptive field centre and surround weighted by the spatial sensitivities of the centre and surround mechanisms and the time course of their responses. Enroth-Cugell and Robson's (1966) recordings from the optic tract (OT) made it clear, however, that this model was only generally applicable to a subset of cells (X-cells), and thus initiated an era of retinal ganglion cell classification parallel to the on-off centre dichotomy. Y-cells revealed a distinct non-linearity in spatial summation by responding to the exchange of a stationary contrast modulated sine-wave grating pattern for a uniform field of the same average luminance irrespective of the phase of the grating. In contrast, for X-cells the grating could be positioned in odd symmetry about the diameter of the receptive field (the 'null' position) so that the exchange evoked no response due to linear summation to zero of signals arising from all parts of the receptive field.

These results have been confirmed and extended principally in the detailed studies of Shapley and colleagues. Hochstein and Shapley (1976a) showed that OT fibres can be dichotomized into X- and Y-types on the basis of their responses to a stationary sine-wave grating pattern whose contrast is modulated sinusoidally in time. X-cells respond almost exclusively at the fundamental (first harmonic) of the modulation frequency. Contrast sensitivity (Hochstein and Shapley 1976a) or response amplitude (Hochstein and Shapley 1976a; Enroth-Cugell et al. 1983) is a sinusoidal function of spatial phase; peak sensitivity or peak response generally occurs when the grating lies in even symmetry about the receptive field centre and the null position is one quarter cycle away. Certain minor X-cell non-linearities in spatial summation are, however, acknowledged. The spatial phase of the fundamental component is independent of contrast only over a limited range (Enroth-Cugell et al. 1983) and sine-wave gratings of low spatial frequency reversed in contrast evoke some response irrespective of spatial phase (Hochstein and

Shapley, 1976a). In addition, small second harmonic responses are recognised as commonly present in X-cells (Hochstein and Shapley 1976a; Enroth-Cugell et al., 1983).

At low spatial frequencies response amplitude and contrast sensitivity of Y-cells are phase-dependent but no null position is found, at a quarter cycle from peak response or peak sensitivity. Y-cells respond transiently at each phase of pattern alternation (Hochstein and Shapley 1976a). Fourier analysis of Y-cell responses at low spatial frequencies yields a dominant first harmonic component whose amplitude is a sinusoidal function of spatial phase, and a second harmonic component which is phase-insensitive. At high spatial frequencies second harmonic distortion dominates the response due to a decline with increasing spatial frequency in the sensitivity of the first harmonic component. The mechanism responsible for these second harmonic responses is distributed throughout and beyond the classical receptive field and has been conceptualised as a population of rectifying subunits each of which sums signals from receptors over an area smaller than the receptive field centre (Hochstein and Shapley 1976b). The modulated second harmonic response of Y-cells to a contrast reversal grating is thought to be due to the synchronous stimulation of these subunits.

1.1.3. Brisk-Sustained/Brisk-Transient Classification

Cleland et al. (1971b, 1973) distinguished sustained and transient cells primarily on the basis of their time-course of response to stimulation of the receptive field centre with a spot of light of appropriate polarity. An initial transient response was elicited in both cell types, but the discharge of sustained cells alone remained above spontaneous activity for the duration of the stimulus. Time course of response to standing contrast is not, however, in itself a particularly robust classifying criterion. Following dark adaptation the responses of retinal ganglion cells become increasingly sustained (Cleland et al. 1973; Iakiela et al. 1976) while in the light-adapted retina responses are predominantly transient (Enroth-Cugell and

Shapley 1973a). Since the degree of light adaptation is said to be a function of receptive field size (Enroth-Cugell and Shapley 1973b), the larger receptive fields of transient cells (section 1.1.4.) could, to some extent, explain their more transient responses. In addition, the responses of cells in the peripheral retina tend to be more transient than those of cells near the area centralis (Cleland and Levick 1974a, Hochstein and Shapley 1976a).

The main contribution of Cleland et al. (1971b, 1973) lay in the association of sustained and transient responses with separate cell types classified on the basis of responses to a battery of tests (see section 1.1.4.). Thus, Cleland (1985) was able to show that the relationship between receptive field size and level of light-adaptation, and that between receptive field eccentricity and response dynamics is valid only for transient units. Cleland and Levick (1974a) described the receptive field properties of a much larger sample of sustained and transient cells which they re-named brisk-sustained (BS-) and brisk-transient (BT-) to emphasize their relatively vigorous responses compared with other recently identified cells with concentric receptive fields (section 1.1.5.).

1.1.4. A Comparison Of X/Y And BS/BT Classification Schemes

There is now little doubt that the X/Y and BS/BT classification schemes are broadly congruous despite the fact that the corresponding tests were not carried out on the same cells.

(a) Responses To Drifting Gratings

Drifting gratings of all effective spatial frequencies evoke a discharge modulated at the temporal frequency of stimulation, about a steady mean in both X-cells (Enroth-Cugell and Robson 1966, Hochstein and Shapley 1976a) and BS-cells (Cleland et al. 1971b, 1973, Cleland and Levick 1974a). The modulated response of Y- or BT-cells at low spatial frequencies gives way at high spatial frequencies

to an unmodulated increase in discharge rate (Enroth-Cugell and Robson, 1966; Hochstein and Shapley, 1976a; Cleland et al., 1971b, 1973; Cleland and Levick, 1974a), which is thought to be due to the non-synchronous stimulation of receptive field subunits (Hochstein and Shapley, 1976b). Unlike BT-cells, BS-cells fail to respond to a radial grating which is symmetrically rotated about the receptive field centre, thus causing no nett change in flux.

Both BS- and BT-cells give orientation-biased responses to drifting gratings of high spatial frequency (Levick and Thibos, 1980a, 1982; Soodak et al., 1987). The elongated dendritic trees (Boycott and Wässle, 1974; Peichl and Wässle, 1981; Wässle et al., 1981b; Leventhal and Schall, 1983) and elliptical receptive fields (Hammond, 1974) of retinal ganglion cells can account for such orientation biases (Levick and Thibos, 1982; Leventhal and Schall, 1983; Soodak et al., 1987).

(b) Spatial Frequency Selectivity And Receptive Field Size

BT-cells have larger receptive field centres than BS-cells, the centre size of both cell types increasing with eccentricity (Cleland et al., 1973; Cleland and Levick, 1974a; Hammond, 1974; Cleland et al., 1979; Peichl and Wässle, 1979). According to Peichl and Wässle (1979), the receptive field centre diameters of BT cells are, at any one eccentricity, 2.5 times larger than those of BS-cells. Spatial resolution is directly related to receptive field centre size (Cleland et al., 1979; Peichl and Wässle, 1979), and X-cells give modulated responses to drifting sine-wave gratings of higher spatial frequency than do Y-cells (Enroth-Cugell and Robson, 1966; Hochstein and Shapley, 1976a,b). The contrast sensitivity of both cell types is a bandpass function of spatial frequency, which declines more abruptly at high than at low spatial frequencies (Lennie, 1980). Optimum spatial frequency is higher for X- than for Y-cells, and X-cells are considerably more sensitive than Y-cells at high spatial frequencies (Lennie, 1980). At low spatial frequencies, Y-cells are slightly the more sensitive though, particularly in X-cells, relative sensitivity to low spatial frequencies increases with increasing temporal frequency (Hochstein and

Shapley 1976a, Victor and Shapley, 1979; Derrington and Lennie, 1982, Enroth-Cugell et al 1983)

(c) Temporal Frequency Sensitivity And Velocity Tuning

One of the main diagnostic features of a BT-cell is a vigorous response to a stimulus of polarity appropriate for the receptive field surround moving at high speed (200 /sec) across the receptive field (Cleland et al 1971b, 1973, Cleland and Levick 1974a). More recent quantitative studies (Lee and Willshaw, 1978, Cleland and Harding, 1983) have demonstrated that the difference in velocity sensitivity of BS- and BT-cells is maintained when centre-activated response are compared. Within each class, BS- and BT-cells have remarkably similar velocity tuning profiles, thus reflecting the lack of variation among X- or Y-cells in spatial and temporal characteristics (Enroth-Cugell and Robson, 1966, Lennie, 1980). In the central retina, BT-cells have higher preferred and upper cut-off velocities than BS-cells. At moderate contrast levels, the response of BT-cells increases as a function of velocity up to 50-100 /sec and declines gradually thereafter, while that of BS-cells peaks at a lower velocity (20-40 /sec) and declines relatively steeply at high velocities. Differences between BS- and BT-cells in preferred and upper cut-off velocity are due almost entirely to spatial factors: when stimulated with drifting gratings of optimum spatial frequency, Y-cells are more sensitive than X-cells only at temporal frequencies above 40Hz, and they are slightly more sensitive at high velocities, presumably because they prefer stimuli of lower spatial frequency (Lennie, 1980). Within the BS and BT classes, upper cut-off velocity increases systematically with receptive field centre size, and hence with eccentricity (Cleland and Harding, 1983). The increase in optimal velocity of BS- or BT-cells as a function of contrast (Cleland and Harding, 1983) is paralleled by a relative improvement with increasing contrast in the sensitivity of X- and Y-cells to medium-to-high temporal frequencies (Shapley and Victor, 1978).

The surround mechanism has also been shown to play a role in determining dif

ferences in the velocity sensitivity of X- and Y-cells. The suppressive effects of the receptive field surround are stronger in X- (BS-) than in Y- (BT-) cells (Ikeda and Wright 1972b; Cleland et al. 1973; Hammond 1975; Bullier and Norton 1979b,c) and this may partially reflect differences in the spatial distribution of the centre and surround mechanisms in the two cell types: the surround mechanism would seem to be spatially more extensive than the centre mechanism in BS- but not in BT-cells (Ikeda and Wright 1972b; Hammond 1975; Bullier and Norton 1979b,c). Additionally, the suppressive effects of the receptive field surround have a shorter latency in X- than in Y-cells (Hamasaki and Cohen 1977). Thus X-cells whose receptive field surrounds have been masked respond strongly to high velocity target motion, while masking of Y-cell surrounds has little or no effect on their velocity sensitivity (Hamasaki and Cohen 1977). The potency of the receptive field surround declines with increase in centre size and hence with eccentricity (Hammond 1975; Bullier and Norton 1979b). In BT-cells the increase in receptive field centre size with eccentricity is accompanied by an overall decrease in sensitivity (Cleland 1983). Thus in the periphery there is no difference in upper cut off velocity between the two cell types (Cleland and Harding 1983); both X- and Y-cells respond well to fast moving stimuli (Cleland and Harding 1983; Hochstein and Shapley 1976a). The substantial overlap in the upper cut off velocity of retinal X- and Y-cells observed by Cohen et al. (1980), which they attribute to the use of stimulus polarity appropriate for the receptive field centre, probably reflects the fact that they pooled results from cells with receptive fields at different eccentricities.

When tested with stationary sinusoidal gratings whose contrast is sinusoidally modulated in time, Y-cells show a relatively steeper decline in sensitivity compared with X-cells as temporal frequency is lowered below the optimum (Shapley and Victor 1978). Although there is some evidence (Lee and Willshaw 1975; Cleland and Harding 1983) that the velocity response curves of Y-cells have steeper ascending slopes than those of X-cells, this difference is not striking, and

when tested with *moving* gratings of optimal spatial frequency, the temporal modulation curves of X- and Y-cells differ trivially (Lennie, 1980).

(d) Peripherally-Evoked Responses

Mcllwain (1964) demonstrated that movement of a small disc in a region remote from the classical receptive field of a retinal ganglion cell evokes a gradual unmodulated increase in maintained firing. This 'periphery effect' was subsequently shown to be strong in BT-cells but weak or absent in Bs-cells (Cleland et al. 1971b, 1973). Mcllwain (1966) also demonstrated short-latency responses in retinal ganglion cells to sudden movement of contours well outside the receptive field. Ikeda and Wright (1972a) made explicit the distinction between the modulated and unmodulated components of the 'periphery effect', both of which could be demonstrated only in BT-cells. A more dramatic effect of peripheral stimulation was discovered by Kruger and Fischer (1973): transient excitatory responses are elicited by the abrupt movement of a large global pattern surrounding but not contiguous with the classical receptive field. This 'shift effect' is strong in Y-cells but weak in X-cells (Barlow et al. 1977; Derrington et al. 1979). The 'shift effect' and both types of 'periphery effect' probably arise from the same mechanism (Fischer et al. 1977; Derrington et al. 1979) which has properties similar to those of Hochstein and Shapley's (1976b) subunits thought to generate the non-linearity of Y-cells. In as far as some X-cells respond weakly to peripheral stimulation they would also be expected to exhibit minor non-linearities in spatial summation.

(e) Encounter Frequency

Due to their large diameter axons (section 1.2), Y-cells are the most commonly encountered units in recordings from the OT (Enroth-Cugell and Robson, 1966). X-cells are encountered more frequently (relative to Y-cells) near the area centralis (Enroth-Cugell and Robson, 1966). In retinal recordings (Cleland and Levick

1974a,b). BS-cells are the units most often encountered near the area centralis with BT-cells relatively more common in the periphery.

(f) Maintained Firing

At equivalent mesopic levels of background illumination, the maintained discharge of BS-cells is higher than that of BT-cells (Cleland et al. 1973) and that of X-cells is higher than that of Y-cells (Lennie 1980).

(g) Direct Tests For Correspondence Between BS- And X-Cells, BT- And Y-Cells

The above comparisons of receptive field properties suggest strongly that BS- and BT-cells distinguished on the basis of their responses to a battery of tests correspond respectively with linear (X) and non-linear (Y) cells. Results from a study in which the corresponding tests were performed on a small sample of individual retinal ganglion cells (Levick and Thibos 1980b) are consistent with this interpretation. However, time course of response to standing contrast is not always correlated with the X/Y dichotomy (Hochstein and Shapley 1976a). In addition, Y-cell responses become increasingly more transient as a function of receptive field eccentricity (Cleland 1983) and stimulus contrast (Shapley and Victor 1978, Lennie 1980). The time course of weak responses of X- and Y-cells at low levels of contrast differs trivially (Lennie 1980).

(h) Axonal Conduction Velocity

BT-cells have on average faster-conducting axons than BS-cells along the myelinated segment of the optic nerve (ON and OT, although the distributions overlap to some extent (Cleland and Levick 1974a). A similar distinction in conduction velocity between retinal afferents of linear (X) and non-linear (Y) *geniculate* cells has also been observed (So and Shapley 1979). A more striking segregation of cell types is seen in the antidromic latencies measured at the ganglion

cell body to stimulation of the OT (Cleland and Levick, 1974a) or the optic chiasm (OX) (Stone and Fukuda 1974), and in retino-geniculate conduction times (Cleland et al., 1971b).

(j) Linear And Non-Linear Sluggish Cells

Cleland and Levick (1974a) subdivided their sustained and transient cells into brisk and sluggish varieties in order to accommodate a previously unrecognised cell type with low responsiveness to visual stimuli which comprised 13% of the the total population. Unlike their brisk counterparts, sluggish sustained (SS) and sluggish-transient (ST) cells could not be distinguished on the basis of relative response modulation to drifting gratings. The most common behaviour was a feeble response modulation which persisted up to the highest effective spatial frequency, though modulated responses to fine gratings were observed in some sluggish cells of both sustained and transient subtypes. More recent quantitative studies have confirmed the implication of these qualitative observations in demonstrating the existence of sluggish units, of both sustained and transient subtypes, with linear or non linear spatial summation (Levick and Thibos 1980; Enroth-Cugell et al., 1983). The discovery of these cell types would not be expected to disrupt the correspondence between BS and X cells, and BT and Y-cells, since sluggish units possess fine axons (section 1.1.7c), it is unlikely that they were encountered in recordings from the OT (Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976a,b). Thus for clarity of exposition, the terms X and Y rather than BS and BT will be retained in subsequent discussion of retinal ganglion cell types.

1.1.5. W-Cells With Concentric Receptive Fields And Sluggish Units

(a) Receptive Field Properties

Stone and Fukuda (1974) abandoned the linearity criterion of Enroth-Cugell and Robson (1966), but persisted with the X-Y classification. The term W-cell was thus used to refer to a rather heterogeneous third group of ganglion cells. Of those with centre-surround receptive field organization, phasic and tonic subtypes were distinguished on the basis of differences in time course of response to standing contrast, which were more striking than those between X- and Y-cells.

In time course of response to standing contrast, tonic W-cells resemble X-cells but show a less prominent initial transient response component and a more regular sustained component, whose magnitude does not decline throughout the duration of stimulus presentation; no inhibition is observed at stimulus offset. Compared with X-cells, tonic W-cells have larger receptive fields at comparable eccentricities and lower spontaneous activity. Though S-cells (Cleland and Levick 1974a) have many properties in common with tonic W-cells, a striking discrepancy which seems to have been overlooked is that sluggish units are by definition weakly responsive, whereas tonic W-cells are said to respond "vigorously" to moving stimuli (Stone and Fukuda 1974).

ST- and phasic W-cells are more closely related. The receptive field centre size of phasic W-cells is within the range of Y-cells, from which they are distinguished by their lower evoked and maintained firing rates and the absence of a periphery effect. Phasic W-cell responses to standing contrast are markedly more phasic than those of Y-cells, though the responses of ST-cells are not obviously more transient than those of their brisk counterparts (Cleland and Levick 1974a).

Stone and Fukuda (1974) briefly remark that phasic W-cells are commonly responsive to fast-moving stimuli, though some are unresponsive to stimulus velocities higher than 50 /sec. None show the vigorous responses to stimuli moving at high

velocity typical of Y-cells. Qualitative observations (Cleland and Levick, 1974a) suggested that both sustained and transient sluggish cells were primarily sensitive to slow movements, though significant responses were evoked by faster speeds of up to 30 /sec. Target motion above 100 /sec was generally ineffective.

A more thorough quantitative analysis of retinal ganglion cell responses to moving stimuli (Lee and Willshaw, 1978) has yielded results not entirely consistent with these early observations. Both sustained and transient subtypes are rather unselective for velocity: response magnitude increases only gradually with increasing velocity from a negligible response at 1 /sec up to a maximum response at 100 /sec. There is some indication of an increase with eccentricity in response magnitude and in the slope of the ascending velocity-response function. Thus the results of this study do not support the common assumption that sluggish cells respond weakly at high stimulus velocities.

Some W-cells (Stone and Fukuda, 1974) or sluggish units (Lee and Willshaw, 1978) give unequal responses to two directions of motion along the same axis through the receptive field, with the degree of asymmetry dependent on stimulus velocity (Lee and Willshaw, 1978). Direction-selective concentric W-cells are, in addition, sensitive to the direction of spot motion along different axes through the receptive field (Stone and Fukuda, 1974), while some sluggish units show orientation-biased responses to drifting gratings of high spatial frequency (Levick and Thibos, 1982).

(b) Axonal Conduction Velocity

As a group, W-cells with concentric receptive fields (Stone and Fukuda, 1974) or sluggish units (Cleland and Levick, 1974a) vary widely in axonal conduction velocity. Their axons are the most slowly conducting, but there is substantial overlap between W- and X populations. Antidromic latencies and retinogeniculate conduction times distinguish more clearly between W- and X-cells. S-cells (Kirk et al., 1975) or tonic W-cells (Stone and Fukuda, 1974) have shorter

latencies than their transient or phasic counterparts. The similarity in axonal conduction velocity of 'concentric' W-cells and sluggish units is a further indication of their functional correspondence.

1.1.6. Retinal Ganglion Cells With Non-Concentric Receptive Fields

Stone and Hoffmann (1972), Stone and Fukuda (1974) and Cleland and Levick (1974b) provided the first detailed description of the response properties of rarely encountered retinal ganglion cells lacking a concentric receptive field organization. While Cleland and Levick (1974b) used distinctive names for these cells, Stone and Hoffmann (1972) and Stone and Fukuda (1974) incorporated them into the W-cell population in order to emphasize their similarity with 'concentric' W-cells, principally with respect to axonal conduction velocity. In the present study the term W-cell will be retained because the cortical projections of the different types within this heterogeneous group have not yet been established.

The majority of rarely encountered units have on-off receptive fields in which an equally strong phasic response can be elicited at light onset and offset, though some cells show a clear asymmetry in the strength of their on and off responses (Stone and Fukuda, 1974; Cleland and Levick, 1974b). No antagonistic region can be demonstrated with annuli, though the relatively weaker response to large compared with small stationary flashed and moving stimuli suggests the presence of a purely inhibitory surround. A subset of these cells is direction-selective (Stone and Fukuda, 1974; Cleland and Levick, 1974b) and directionally-tuned (Stone and Fukuda, 1974), with a similar range of effective directions for either stimulus polarity. Directionally selective responses are strongest at low velocities, and stimulus speeds above 50 /sec are ineffective. Suppressed-by-contrast cells (Rodieck, 1967) have a considerable spontaneous activity which is suppressed by the presence of a contrast (particularly in the form of a grating) within the receptive field. Finally, a minority of cells with concentric centre-surround receptive field organization are 'colour-coded' (Cleland and Levick, 1974b).

1.2. MORPHOLOGY OF PHYSIOLOGICALLY IDENTIFIED RETINAL GANGLION CELLS

There are clear physiological grounds for distinguishing X- and Y-cells and a rather heterogeneous third group. The question of whether differences in receptive field properties and axonal conduction velocity are reflected in underlying morphology is particularly important since cell proportions, retinal distribution and central projections can be established more reliably with morphological techniques.

Boycott and Wassle (1974) were the first to provide a clear morphological substrate for the X-, Y-, W-classification of retinal ganglion cells. By developing a whole-mount Golgi-stained retinal preparation they were able to discern four distinct morphological types of ganglion cell which they termed α, β, γ and δ. On the basis of dendritic field size, soma and axon diameter of morphological types in comparison with known physiological characteristics of X-, Y- and W-cells, Cleland and Levick (1974a) and Stone and Fukuda (1974) argued for a correlation between α- and Y-cells, β- and X-cells and γ- and W-cells.

While qualitative comparisons of morphological and physiological properties are suggestive, quantitative comparisons are discouraging. Shrinkage of the whole-mount preparation (Wassle et al. 1978) while, on the one hand, reducing a discrepancy between the β-cell dendritic field diameter and X-cell receptive field centre size, serves to disrupt the apparently remarkable congruence between Y-cell receptive field centre sizes and the diameter of α-cell dendritic fields. Additionally, the dendritic fields of γ-cells are not well matched to the centre sizes of W-cell receptive fields and such a discrepancy is accentuated when shrinkage is acknowledged. The above comparisons are complicated by the different methods used to measure receptive field centre size (cf. Peichl and Wassle, 1979) and the fact that retinal ganglion cells tend to have elliptically shaped receptive fields (Hammond, 1974) and elongated dendritic trees (Boycott and Wassle, 1974; Peichl and Wassle, 1981; Wassle et al., 1981b; Leventhal and Schall, 1983).

More reliable evidence relating physiology and morphology derives from a series of elegant experiments by Wassle and colleagues. By comparing perikaryal sizes at comparable eccentricities Wassle et al (1975a) produced powerful evidence that the large ganglion cells of cresyl violet preparations correspond to the Golgi stained α-cells of Boycott and Wassle (1974). This suggestion has subsequently been confirmed by Wassle et al (1981a), who employed a modified neurofibrillar staining technique to allow quantitative treatment of dendritic trees and perikarya in the same preparation. The earlier work of Wassle et al (1975) enabled Cleland et al (1975a) to carry out a direct test for correspondence between α- and Y-cells. By recording from all Y-cells within a small patch of retina and comparing their receptive field positions with the location of α-cells identified in retinal whole mounts, they demonstrated an almost perfect correlation between physiological and morphological types. An even closer match between physiological and histological maps is found when recording site rather than receptive field centre is compared with soma position (Fukuda and Wassle 1981). There is thus no doubt that α-cells are the morphological counterparts of Y-cells. They represent approximately 4% of the total retinal ganglion cell population. Peak density is greatest and soma size smallest at the area centralis; peak density decreases and soma size increases monotonically with increasing eccentricity. Their absolute frequency is greatest at the area centralis, but they are relatively more common in the periphery (Wassle et al 1975, 1981a).

The direct test for correspondence employed by Wassle and colleagues is reliable only for α-cells, since they have a large inter-cell distance and are numerically infrequent. However intracellular staining with Lucifer yellow in eye-cup preparations (Saito, 1983a,b) or HRP in vivo (Stanford and Sherman 1983) into physiologically identified retinal ganglion cells has confirmed that β-cells are the morphological counterparts of X-cells. Some W-cells are indeed γ-cells (Stanford and Sherman 1983, Saito, 1983a,b) which comprise 40% of the total ganglion cell population and are concentrated in the area centralis (Illing and Wassle 1981). Others correspond to a morphological cell type recognised only recently (Leventhal et al

1980; Stone and Clarke, 1980; Leventhal, 1982) with a dendritic arbor similar to that of α-cells but a soma size in the range of β-cells (Stanford and Sherman, 1983). Thus, Wassle et al's (1981b) estimate that β-cells comprise 55% of the ganglion cell population is almost certainly too high, since cell identification rested heavily on cell body size. When medium-sized W-cells are taken into account, the estimated proportion of β-cells falls to 40–45% (Leventhal, 1982). They are concentrated in the area centralis but at all eccentricities they have the highest cell density.

PART II: VISUAL THALAMIC RELAY NUCLEI

Implicit in the classification of retinal ganglion cells is the assumption that different cell types subserve different functional roles. The distinction between retinal ganglion cells in receptive field properties and receptive field size, retinal distribution, axonal calibre and conduction velocity, perikaryal size and dendritic morphology is indicative of major functional differences. Further support for this notion derives from their different central projections.

The direct route from the retina to the visual cortex is via a thalamic relay which includes the laminated part of the dorsal lateral geniculate nucleus (dLGN), the medial interlaminar nucleus (MIN), and the retinal recipient zone (RRZ) of the pulvinar. The ventral lateral geniculate nucleus (vLGN) receives retinal afferents but does not project to the visual cortex.

1.3. THE DORSAL LATERAL GENICULATE NUCLEUS

1.3.1. Excitatory Retinal Inputs

Of the retinal terminations in the visual thalamus those in the dLGN are by far the heaviest and best analysed. The majority of dLGN neurones receive their excitatory input from one or a few retinal ganglion cells of the same functional type; there is no convergence of on- or off-centre and little mixing of brisk sustained (BS) and brisk-transient (BT) pathways (Cleland et al., 1971a,b). Wilson and Stone (1975) and Wilson et al. (1976) demonstrated that some geniculate cells had W-type receptive field properties, and orthodromic latencies to ON and OX stimulation indicative of monosynaptic input from retinal W-afferents. Cleland et al. (1975b, 1976) also described sluggish units in the dLGN with a long latency retinal input.

The above results led Cleland et al (1971a,b, 1976) to attempt a classification of geniculate neurones using the same criteria they had employed to differentiate between retinal ganglion cells. The majority of units could be classified as BS or BT, though they experienced using their 'battery of tests' approach much more difficulty in obtaining clear-cut results at the geniculate level. Not only are there differences between geniculate cells and their retinal counterparts, but there is also a certain amount of variation in the receptive field properties of geniculate cells of the same functional group. Thus in order to appreciate the contribution made by the geniculate input to the generation of receptive field properties in areas 17 and 18, it is vital to examine the properties of geniculate cells themselves.

In Nissl stains three layers are readily apparent in the dLGN: the dorsal lamina A which receives a projection from the contralateral eye; the intermediate lamina A1 which receives a projection from the ipsilateral eye; and the lower lamina B, which can be divided into a number of laminae on the basis of differential input from the two eyes (Guillery, 1970; Hickey and Guillery, 1974). lamina C receives input from the contralateral eye; lamina C1 from the ipsilateral eye; and lamina C2 from the contralateral eye. The most ventral lamina, lamina C3 has no detectable retinal input. Lamina C and C1-C3 are termed the C-laminae or the ventral layers while the A-laminae are referred to as the dorsal layers.

(a) The Dorsal Laminae

The A laminae contain only X- and Y-cells (Wilson et al., 1976; Bullier and Norton, 1979a; Sretavan and Hoffmann, 1979; Friedlander et al., 1981; Mowshon, 1981). The small number of sluggish cells with long latency retinal input recorded by Cleland et al. (1976) may have been BS-cells; the much greater variability in the responsiveness of units in the dLGN compared with the retina obscures the distinction between brisk and sluggishly responding neurones in that nucleus (Cleland et al., 1976). Further, the A laminae receive retinal input exclusively from α- and β-cells (Illing and Wassle, 1981; Leventhal, 1982), and via termi-

nal branches of axons which are much coarser than those which innervate the parvocellular C-laminae (Mason and Robson 1979), where only W-cells are encountered. X-cells are located almost exclusively in the A-laminae, where they are encountered more frequently than Y-cells (Wilson et al. 1976, Cleland et al. 1976, So and Shapley 1979, Friedlander et al. 1981, but see Sur-Kranz and Hoffmann 1979). The relative frequency of Y-cells in the dLGN increases with eccentricity (Cleland et al. 1971b, Hoffmann et al. 1972, Dreher and Sefton, 1979, So and Shapley, 1979), reflecting a similar trend in the retina. The estimated Y/X cell ratio in the dorsal laminae (So and Shapley, 1979, Friedlander et al. 1981) is greater than the ratio of α/β cells projecting to lamina A and A1 (Leventhal 1982), and reflects a greater divergence along the Y pathway (Sur and Sherman 1982a, Bowling and Michael, 1984). Within the dorsal laminae, the proportion of Y-cells is greater in lamina A1, though the α/β cell ratio is higher for projections to lamina A (Leventhal 1982). The amplification of the Y system would thus seem to be more intense in lamina A1. An analysis of local potentials evoked in the dLGN by electrical stimulation of the optic disk (OD) or OX [Current Source Density (CSD) Analysis, Mitzdorf and Singer 1977] indicates that short-latency activity associated with Y input is relatively stronger in lamina A1 than in lamina A, whereas X-activity is stronger in lamina A. There is some evidence for a partial dorso-ventral segregation of X- and Y-afferents respectively within laminae A and A1 (Mitzdorf and Singer 1977, Bowling and Michael 1984), though this has been disputed (Sur and Sherman 1982a, Humphrey et al. 1985a).

(b) The Ventral Laminae

Within the dLGN, W-cells are found predominantly (Cleland et al. 1976) or exclusively (Wilson et al. 1976, Stanford et al. 1983) in the ventral laminae. Thus, early electrophysiological studies (Fukuda and Stone 1974) and anatomical experiments (Kelly and Gilbert 1975) failed to demonstrate a retinal projection from W-cells to dLGN because stimulation sites for antidromic invasion and injection sites for retrograde transport of HRP were located in the A-laminae.

The prominent input to the ventral laminae is fast activity arriving in lamina C (Mitzdorf and Singer, 1977), which arises via axon collaterals of Y OT fibres innervating lamina A (Bowling and Michael, 1980, 1984; Sur and Sherman, 1982a). In lamina C, Y-cells are encountered relatively more frequently than in the A-laminae (Cleland et al., 1976; Wilson et al., 1976). Lamina C also receives a rather less prominent input from slowly conducting afferents with a wide range of conduction velocities (Mitzdorf and Singer, 1977). Concentric W-cells are encountered as frequently as Y-cells in lamina C and a small proportion of cells with non-concentric receptive fields have also been recorded there (Cleland et al., 1976; Wilson et al., 1976). No significant X-input to lamina C is revealed by CSD analysis (Mitzdorf and Singer, 1977). A minority of X OT axons projecting to lamina A have, however, been shown to send a few collateral branches to lamina C (Sur and Sherman, 1982a), and a small number of X-cells have been recorded there (Wilson et al., 1976; Cleland et al., 1976). According to Wilson et al. (1976), Mitzdorf and Singer (1977) and Stanford et al. (1983), there is a clear-cut separation between Y- and X-cells recorded dorsally, and W-cells encountered in the ventral part of lamina C. This is paralleled by an anatomical segregation based on cell body size (Hickey and Guillery, 1974): the dorsal part of lamina C contains large cells, while ventrally there is a preponderance of small cells, which are similar in size to those comprising laminae C1–C3. These layers characteristically contain only small cells and are collectively referred to as the parvocellular C-laminae. In single unit studies, no X- or Y-cell has been recorded in the parvocellular C-laminae (cf. Wilson et al., 1976; Cleland et al., 1976; Stanford et al., 1983). However, a weak Y-input to C1 has been identified in CSD analysis (Mitzdorf and Singer, 1977) and, contrary to earlier reports (Mason and Robson, 1979; Leventhal, 1982; Sur and Sherman, 1982a), some ipsilateral Y-fibres have been seen to terminate in C1 (Bowling and Michael, 1984). The retinal input to the parvocellular C-laminae arrives almost exclusively from fine calibre axons of similar size to the thin axons which innervate lamina C (Mason and Robson, 1979). Compared with lamina C, the parvocellular C-laminae receive a much weaker retinal input from

slowly conducting fibres (Mitzdorf and Singer, 1977) and contain a greater proportion of cells with non-concentric receptive fields (Wilson et al., 1976; Cleland et al., 1976). As in the retina, the majority of W-cells in the dLGN have concentric receptive fields (Wilson et al., 1976; Cleland et al., 1976), though all subtypes of W-cell are found. Direction selective units, the only W subtype not encountered in the dLGN by Wilson et al. (1976) or Cleland et al. (1976), have more recently been identified in the nucleus (Stanford et al., 1981); they form a proportion of those W-cells responsive only to slow movement.

The major W input to the C-laminae originates from medium sized cells with wide-spreading dendrites (Rowe and Dreher, 1979; Leventhal, 1982). Leventhal (1982) estimates that X-cells comprise only 5% of the input to a single parvocellular C-lamina. The medium-sized ganglion cells providing the major input to the parvocellular C-laminae have been subdivided on the basis of differences in dendritic morphology and differential sites of projection within the thalamus (Leventhal, 1982).

1.3.2. Morphological Correlates Of Physiologically Identified Cells In The dLGN

Investigations of cortical projections of dLGN cells using anatomical techniques have relied on indirect methods which take advantage of the partial laminar separation of cell types within the dLGN and differences in the size of their somata and axons. The functional interpretation of geniculo-cortical projections disclosed by neuroanatomical techniques (see Chapter 2) rests on a correlation between anatomically and physiologically identified cell types in the dLGN. Structure/function correlations in the dLGN have recently assumed an added significance with the demonstration of the cortical projections of dLGN cells identified on the basis of their entire dendritic field morphology (Meyer and Albus, 1981b; see Chapter 2).

LeVay and Ferster (1977), following Wilson et al. (1976), used several converging lines of indirect evidence to suggest that the morphological classes 1, 2 and 3 of Guillery (1966) correspond respectively to Y cells, X-cells and interneurones. Wilson et al. (1976) proposed a correlation between class 3 and W-cells since both are confined to the C laminae.

A more precise structure/function relationship for dLGN cells has been determined more recently by means of the iontophoretic ejection of HRP into physiologically characterized neurones (Friedlander et al. 1979, 1981; Stanford et al., 1981, 1983; Weller and Humphrey, 1985). From these studies it has emerged that most, if not all, class 1 cells are Y-cells; they are large with thick cruciate dendrites which typically cross laminar borders and possess only a few simple, spinelike dendritic appendages. Many X-cells have class 2 morphology; they are intermediate in size and possess sinuous dendrites, finer than those of class 1 cells, with numerous grapelike dendritic appendages clustered at or near dendritic branch points. Some Y-cells have a pattern of dendritic morphology with characteristic class 2 features (for example, grapelike clusters at dendritic branch points). Compared with class 2 X-cells, class 2 Y-cells tend to have slightly larger somata, thicker axons and wider diameter dendritic fields. In addition, the dendritic tree of class 2 Y-cells is circular and, like that of its class 1 counterpart, typically crosses laminar borders. X-cell dendrites are elongated along projection lines but confined within a single lamina. All cells with class 3 morphology which have been recovered in structure/function studies of the dLGN have been identified physiologically as X-cells (Friedlander et al., 1979, 1981; Weller and Humphrey, 1985). Compared with their class 2 counterparts, class 3 X-cells have smaller somata, thinner tortuous dendrites and more complex dendritic appendages. Three of the 12 X-cells recovered by Weller and Humphrey (1985) had medium sized somata but, in other respects, class 1 morphology. These cells probably correspond to the morphologically unclassified cells of Friedlander et al. (1981), which were considered too small to be class 1 cells.

Class 4 cells, though differentiable into a number of subtypes (see also Meyer and Albus, 1981b), are the morphological correlates of W-cells (Stanford et al., 1981, 1983). They are intermediate in size and are characterized by dendritic arbors oriented parallel to geniculate laminae.

I.3.3. Inhibition In The dLGN

An assessment of the significance of geniculate input for the generation of receptive field properties in areas 17 and 18 requires extensive quantitative data on the response characteristics of dLGN cells, since both spatial and temporal integration occur at the geniculate level (Hubel and Wiesel, 1961; Cleland et al., 1971a,b). Moreover, it is clear that the excitatory input to dLGN cells is modulated by powerful inhibitory influences. Inhibitory postsynaptic potentials (IPSPs) are evoked in dLGN cells by electrical stimulation of the optic disc (OD) and optic tract (OT) (Lindstrom, 1982), the optic chiasm (OX) and the optic radiations (OR) (Singer and Bedworth, 1973), the visual cortex (Lindstrom, 1982), and by visual stimulation (Singer and Creutzfeldt, 1970; Singer et al., 1972; Singer and Bedworth, 1973). Recent experiments have clarified that relay cells in the dLGN are subject to at least two types of postsynaptic inhibition: a feed forward inhibition arising from retinal ganglion cells, and a recurrent collateral inhibition (Singer and Bedworth, 1973; Dubin and Cleland, 1977; Lindstrom, 1982). The feed forward pathway is disynaptic and the inhibitory neurone is intrinsic to the dLGN. The recurrent system starts with axon collaterals of relay cells and the inhibition is mediated by perigeniculate neurones located in a loosely organized nucleus above lamina A of the dLGN (Dubin and Cleland, 1977; Ahlsen and Lindstrom, 1982).

Perigeniculate neurones are either X-like or Y-like and possess binocular non-concentric on/off receptive fields, properties which reflect a convergent input from on- and off-centre relay cells of either the X- or Y-type (Ahlsen et al., 1983). Similarly, there is little mixing of X- and Y-pathways back to the dLGN (Lindstrom and Wrobel, 1984).

Class 3 cells are thought to be the interneurones which participate in the classic triadic arrangements in dLGN and thus mediate feed-forward inhibition from retinal ganglion cells. Famiglietti and Peters (1972) implicated the dendritic appendages of class 3 cells (Guillery, 1969) as the source of processes lying postsynaptic to retinal axon terminals in the synaptic glomerulus. These processes receive retinal synapses and, on the basis of the shape of their synaptic vesicles, are thought to make synaptic contact with relay cells (Famiglietti, 1970). In addition, they are immunoreactive for glutamate acid decarboxylase (GAD) (Fitzpatrick et al. 1984), the synthesizing enzyme for gamma-aminobutyric acid (GABA), which is an inhibitory neurotransmitter in the thalamus (Curtis and Tebecis, 1972). There are a number of morphological similarities, such as small somata and elongation of dendrites along projection lines, between GAD immunoreactive and class 3 neurones in the A laminae of the dLGN (Fitzpatrick et al., 1984).

Friedlander et al. (1981) have questioned the assumption that interneurones exist as a unique cell class in the main laminae of the dLGN: some of their sample of class 3 neurones were confirmed relay cells as demonstrated by their antidromic activation from the visual cortex and the course of their axons into the OR. On the other hand, there is no evidence for direct excitatory or inhibitory connections between geniculate relay cells (Lindstrom, 1982). Since GAD positive neurones are distinguishable from other small to medium sized cells in the A-laminae by their failure to label following injection of HRP into the visual cortex (Fitzpatrick et al. 1984), it is likely that class 3 cells can be subdivided into interneurones and relay cells.

The apparent discrepancy between the correspondence of class 3 and X-cells (Friedlander et al., 1979, 1981, Weller and Humphrey, 1975) and Dubin and Cleland's (1977) report of both BS- and BT-classes of interneurone can be only partially reconciled by considering the lack of correlation between cell classifications based on linearity of spatial summation and time course of response to standing contrast, particularly in the dLGN (see 1.3.4.). In any event, if all in-

trinsic interneurones are X cells, one is confronted with the problem of finding a suitable interneurone to mediate the shortest-latency IPSPs evoked in geniculate cells by stimulation of the OT (Singer and Bedworth, 1973; Lindstrom, 1982). One would expect a fast input from Y retinal axons to cause class 3 geniculate interneurones to fail tests of linearity of spatial summation. Yet X-cells by definition behave linearly in this respect. Accordingly, no geniculate X-cell has been shown to receive convergent excitatory input from X- and Y retinal afferents (Wrobel and Lindstrom, 1984). The claim that perigeniculate nucleus neurones receive a monosynaptic input from Y-cells in the retina (Schmielau, 1979) remains unsubstantiated while a disynaptic recurrent pathway via axon collaterals of relay cells and a perigeniculate interneurone is too slow to account for the shortest-latency IPSPs in relay cells (Lindstrom, 1982). Permanently many of the presumed inhibitory terminals on the dendrites of X- and particularly of Y-cells in the dLGN do not participate in the classic triadic complex (Wilson et al., 1984). In the light of the above considerations, it seems necessary to assume that at least some of these terminals derive from the axons of Y-cells intrinsic to the dLGN, rather than from the axons of perigeniculate neurones. By the same token, geniculate X-cells may participate not only in dendro-dendritic but also in axo-dendritic inhibition within the dLGN.

Until recently, inhibitory action within the dLGN was thought to be relatively specific to X-cells. The physiological evidence discussed below suggests that inhibition is more marked along the X- than the Y-channel. Additionally, the processes of relay cells that enter the synaptic complexes are considered to be grape-like dendritic appendages characteristic of class 2 cells, which have been associated on the basis of indirect evidence (LeVay and Ferster, 1977) with X-cells. Indeed, Wilson et al. (1984) have recently confirmed that class 2 X-cells differ from class 1 Y-cells in commonly exhibiting triadic arrangements. However, the Y-cells with class 2 morphology (Friedlander et al., 1979, 1981) presumably also participate in such triads and conceivably differ in response properties from class 1 Y-cells. Indeed, the inter- and intra-laminar differences in Y-cell properties to be reported

below may well be correlated with differences in underlying morphology. The possibility that class 1 and class 2 Y-cells differ in response properties is of interest given their differential projections to areas 17 and 18 (see Chapter 2). Pertinently there is now good evidence for substantial heterogeneity in the response properties of X-cells in the dLGN, which is associated with differences in retino-geniculate circuitry. Some X-cells in the dLGN exhibit relatively long latencies of response to visual stimulation (Mastronade, 1983, 1987a; Humphrey and Weller, 1985) due to potent feed-forward inhibition from retinal ganglion cells (Mastronade, 1987b), and preliminary evidence suggests that such 'lagged' X cells have class 2 morphology (Weller and Humphrey, 1985).

1.3.4. Receptive Field Properties Of Geniculate X-, Y- And W-Cells: A Comparison With Retinal Ganglion Cells

Authors who have compared response properties of retinal ganglion cells and lateral geniculate neurones have reported in the dLGN: spatial filtering (Hubel and Wiesel, 1961; Hammond, 1973; Maffei and Fiorentini, 1973; Lee et al., 1981; Troy, 1983a, but see Bullier and Norton, 1979b) and temporal filtering (Lee et al., 1981; Troy, 1983b), together with an enhancement of the small but reliable differences in velocity tuning of X- and Y-cells in the retina (Singer and Bedworth, 1973; Frishman et al., 1983).

A more direct approach is to record from dLGN neurones and simultaneously from OT fibres (Singer et al., 1972) or retinal ganglion cells (Cleland and Lee, 1985) providing their retinal input, or from synaptic 'S' potentials (Hubel and Wiesel, 1961; So and Shapley, 1979, 1981; Lee et al., 1981; Kaplan and Shapley, 1982; Cleland et al., 1983), which represent the arrival of impulses in a retinal afferent (Kaplan and Shapley, 1984). These techniques control for variation in response properties with eccentricity, response variability over time, and for changes in the physiological condition of the preparation.

(a) Linearity Of Spatial Summation

The distinction between X- and Y-cells based on the linearity of spatial summation is maintained in the dLGN (So and Shapley, 1979; Shapley and Hochstein, 1975; Kratz et al., 1978a; Derrington and Fuchs, 1979; Lehmkuhle et al., 1980) and is correlated with the classification of Cleland et al. (1971) and Hoffmann et al. (1972) based on responses to a battery of tests (Kratz et al., 1978a). Significantly Y-cells in lamina C give much greater second harmonic responses than those in the A laminae (Frascella and Lehmkuhle, 1984). As in the retina, both linear and non-linear W-cells have been recorded in the dLGN (Sur and Sherman, 1982b).

An inhibitory convergence in dLGN of Y- onto X-cells (Singer and Bedworth, 1973) might be expected to cause certain non-linearities of spatial summation even in geniculate cells that receive excitatory retinal input from X-cells. However, cells in dLGN which receive X retinal afferents show linear spatial summation (So and Shapley, 1979). The weak frequency-doubled inhibition in the responses of many geniculate X-cells to a contrast reversal grating (So and Shapley, 1979) disappears at high spatial frequencies at which Y-cell second harmonic responses are predominant. In fact, recent studies have found little evidence for inhibitory interaction between X- and Y-cells either along the feed-forward or feed-back pathways (Lindström and Wróbel, 1984; Mastronade, 1987b).

(b) Peripherally-Evoked Responses

As in the retina, Y-cells in the dLGN show a periphery (Cleland et al., 1971b) or 'shift' effect (Fischer and Krüger, 1974). Interestingly, Fischer and Krüger (1974) report that, whereas in the retina the 'shift effect' is only excitatory, in the dLGN it can be either excitatory or inhibitory.

(c) Spatial Characteristics

Direct comparisons of geniculate cells and their retinal afferents have demon-

strated in dLGN selective attenuation in responses to stimuli of low spatial frequency (Hubel and Wiesel, 1961; Singer et al., 1972; Lee et al., 1981; Cleland and Lee, 1985), which is more pronounced for X- than for Y-cells (Lee et al., 1981; Cleland and Lee, 1985). This is consistent with Hammond's (1973) observation of an increase in surround potency at the geniculate level in simultaneous recordings in dLGN from a tonic cell and EPSPs from one of its retinal fibre inputs. According to Cleland and Lee (1985), magnitude of low frequency attenuation is proportional to contrast. This may partially explain the results of So and Shapley (1981) who emphasize the overall similarity in the spatial tuning of dLGN cells and their retinal inputs.

The differential sensitivity of X- and Y-cells to stimuli of low spatial frequency is far more pronounced in the dLGN than in the retina. Compared with Y-cells, X-cells show a relatively steeper decline in contrast sensitivity as spatial frequency is lowered below the optimum (Lehmkuhle et al., 1980; Troy, 1983a). In addition, a relative improvement in low spatial frequency sensitivity with increasing temporal frequency is observed in all Y-cells but only a minority of X-cells (Troy, 1983b). X-cells are more sensitive than Y-cells at high spatial frequencies, and their optimal spatial frequencies are higher (Troy, 1983a). Y-cells have a higher peak contrast sensitivity than X-cells (Troy, 1983a), and Y-cells situated in the C-lamina are more sensitive than those in the A-lamina, particularly at low spatial frequencies (Frascella and Lehmkuhle, 1984).

As in the retina, X-cells have a higher spatial resolution than Y-cells at comparable eccentricities (Derrington and Fuchs, 1979; So and Shapley, 1979; Troy, 1983a). Y-cells in the dLGN show non-linear (second harmonic) responses to fine contrast-modulated spatial gratings (So and Shapley, 1979; Lehmkuhle et al., 1980), but seldom respond with an elevation of mean discharge rate to a high spatial frequency drifting grating (Cleland et al., 1971b; Hoffmann et al., 1972). Among Y-cells in the dLGN, those in lamina C and the ventral part of A1 have the lowest spatial resolution (Movshon, 1981). This may partly reflect the fact that distribu-

tion of Y-cell synaptic terminals is broader and denser at the bottom than at the top of the A-laminae (Bowling and Michael, 1980, 1984). The inter- and intralaminar differences in Y-cell properties are of interest in view of the differential projections to areas 17 and 18 from different parts of the dLGN (see Chapter 2).

The width distribution of terminal boutons from X-axons is constant across and between the A-laminae (Sur and Sherman, 1982a; Bowling and Michael, 1984). Thus, the reported higher spatial resolution of X-cells in lamina A compared with those in lamina A1 (Sireteanu and Hoffmann, 1979; Troy, 1983a, but see So and Shapley, 1979; Lehmkuhle et al., 1980) is best explained by differential X afferent input to the two A-laminae rather than differences in excitatory convergence. The lower cell density in the temporal retina (Wassle et al., 1977; Cleland et al., 1977a) which provides the input to lamina A1, could be compensated by larger receptive fields with lower spatial resolution (Sireteanu and Hoffmann, 1979). ON- and X-cells projecting ipsilaterally have larger dendritic fields than those projecting contralaterally (Leventhal, 1982). Bullier and Norton (1979a,b) conclude that geniculate X-cells with large receptive fields and weak antagonistic surrounds are probably driven by X retinal ganglion cells with similar receptive field properties.

Linear and non-linear W-cells do not differ in contrast sensitivity or spatial resolution, both of which are poorer at comparable eccentricities than those of X- and Y-cells (Sur and Sherman, 1982b). Unlike X-cells, linear W-cells display no sensitivity loss at low spatial frequencies, contrast-sensitivity functions decline monotonically with increasing spatial frequency. Non-linear W-cells differ from Y-cells in that the non-linear component is more sensitive than the linear component over the entire spatial frequency range.

(d) Temporal Characteristics And Velocity Tuning

Geniculate cells are less sensitive at all temporal frequencies than their retinal counterparts (Troy, 1983b), but the decline in sensitivity is greatest for low temporal frequencies (Kaplan and Shapley, 1982; Lee et al., 1981). At their respective

optimum spatial frequencies. Y-cells are more sensitive than X-cells at all temporal frequencies (Troy 1983b), with the most sensitive Y-cells located in lamina C (Frascella and Lehmkuhle, 1984). Since geniculate X- and Y-cells are not obviously distinguished by their temporal contrast sensitivity curves (Troy 1983b) while in the retina, X-cells are more sensitive than Y-cells to low temporal frequencies (Shapley and Victor, 1978), low temporal frequency filtering would seem to be more marked along the X channel. Permutently So and Shapley (1979) reported that although linear (X) cells in dLGN receive retinal input from sustained cells, a greater proportion of prepotentials in the initial transient give rise to a cell spike than in the later sustained component. More recent work has indicated, however, that this conclusion can apply only to a subset of X-cells. In lagged X-cells, stimulation of the receptive field centre with a stationary spot of light elicits strong inhibition followed by well-sustained excitation (Mastronade, 1983, 1987a; Humphrey and Weller, 1985). A decrease in stimulus contrast leads to an improvement in signal transmission at the retino-geniculate synapse and more sustained responses in the dLGN (Cleland and Lee, 1985). Thus, at the geniculate level the time course of response to standing contrast is not a good indicator of whether a cell is X or Y (Shapley and Hochstein, 1975; So and Shapley, 1979; Bullier and Norton, 1979a,b).

As in the retina, Y-cells are capable of slightly higher temporal resolution than X-cells when responses to stimuli only of optimum spatial frequency are compared (Lehmkuhle et al., 1980). However, the temporal resolution of Y cells in lamina C and the ventral part of lamina A1 is higher than that of other Y cells (Movshon, 1981) while lagged X-cells have relatively low temporal resolution compared with other X-cells in the dLGN (Humphrey and Weller, 1985; Mastronade, 1987a).

The temporal resolution of W-cells varies widely but is occasionally very high (Movshon, 1981; Sur and Sherman, 1982b); it is determined for both subtypes by the linear component (Sur and Sherman, 1982b). Linear W-cells are more sensitive than non-linear W-cells at all temporal frequencies.

As in the retina, differences in velocity tuning of X- and Y-cells in dLGN are determined predominantly by spatial factors (Frishman et al., 1983; Cleland and Lee, 1985), reflecting the similarity in the temporal modulation sensitivity curves of the two cell types (Lehmkuhle et al., 1980; Troy, 1983b). Comparisons of response properties of geniculate cells and ganglion cells afferent to them (Cleland and Lee, 1985) indicate that no radical change in velocity tuning occurs at the geniculate level. A few cells show selective response attenuation at low or high speeds but these modifications of velocity tuning occur across the X/Y classification thus blurring a clear distinction observed at the retina.

(e) Other Properties

dLGN neurones are more selective for stimulus length than their retinal afferents (Cleland et al., 1983) and the magnitude of response attenuation for long stimuli is dependent on stimulus orientation. However, the claim that the orientation biases in the responses of retinal ganglion cells to drifting gratings of high spatial frequency are enhanced in the dLGN (Vidyasagar and Urbas, 1982) has recently been refuted (Soodak et al., 1987).

The maintained activity of X- and Y-cells in the dLGN is lower than that of their counterparts in the retina. If this attenuation is due to a tonic inhibitory influence of the spontaneous activity of retinal ganglion cells (Suzuki and Ichijo, 1967), it is not surprising that it is greater for X- than for Y-cells (Fukuda and Stone, 1976; Bullier and Norton, 1979a,b).

It is generally believed that intrinsic interneurones are responsible for shaping the receptive field properties of geniculate cells (Singer, 1977), while perigeniculate cells may regulate the gain of transmission through the dLGN according to the level of arousal (Ahlsen et al., 1985). However, spatial and temporal filtering in the dLGN are dependent on synchronised slow activity in the EEG (Kaplan and Shapley, 1982), while electrical stimulation of the midbrain produces a decrease

in the inhibitory strength of the receptive field surround and an increase in maintained activity (Fukuda and Stone, 1976). Thus, the function of inhibition in the dLGN may be to modulate the transmission of information through the nucleus during variations in states of arousal. It may be unwise to assume that the increased filtering along the retino-geniculate pathway observed in anesthetized preparations necessarily applies in the alert cat.

I.4. THE MEDIAL INTERLAMINAR NUCLEUS

The MIN is a cytoarchitecturally distinct zone of the visual thalamus, which is located adjacent and medial to the laminated part of the dLGN and receives a separate retinotopic projection (Sanderson, 1971). The majority of neurones encountered in MIN resemble Y-cells in the laminated dLGN both in receptive field properties (Mason, 1975; Dreher and Sefton, 1975, 1979; Palmer et al., 1975; Kratz et al., 1978b) and in their short latencies to orthrodromic stimulation of the OX and antidromic stimulation of the visual cortices (Palmer et al., 1975; Kratz et al., 1978b; Dreher and Sefton, 1979). However, in some respects MIN Y-cells add to the variation in Y cell properties in the thalamus. At comparable eccentricities, Y-cells in the MIN have larger receptive fields than those in the laminated dLGN (Kratz et al., 1978b; Dreher and Sefton, 1979), and thus might be expected to prefer higher stimulus velocities. According to Kratz et al. (1978b) the increase in receptive field size with eccentricity is much steeper for Y-cells in the MIN than those in the dLGN, though Dreher and Sefton (1979) report contradictory findings. Y-cells in the MIN have shorter mean orthodromic conduction latencies than those in the dLGN (Kratz et al., 1978b; Dreher and Sefton, 1979). According to Dreher and Sefton (1979), these differences in conduction latency reflect differences in axonal conduction velocity. However, of the Y OT axons that innervate the laminated dLGN, most (Sur and Sherman, 1982a) or all (Bowling and Michael, 1980, 1984) send collateral branches to the MIN.

Rowe and Dreher (1982) estimate that approximately 50% of retinal ganglion cells projecting to the MIN are α Y-cells. The much higher encounter frequency of Y-cells in the MIN can be attributed to a high degree of divergence along the Y pathway, similar to that observed in the main layers, rather than simply reflecting electrode bias. The overwhelming majority of degenerating retinal afferents observed in the MIN are coarse and lie among cells similar in size to the largest cells of the main layers (Guillery et al. 1980). By far the most commonly found cell type in the MIN in Golgi preparations (Szentágothai 1973) and following HRP injections into the OR or specific visual areas (Meyer and Albus 1981; Raczkowski and Sherman 1983) has dendritic morphology and axonal caliber similar to class I cells in the main layers. The majority of these have bipolar dendrites oriented in parallel with the main axis of the MIN, corresponding to the arrangement of terminal boutons of retinal Y axons (Bowling and Michael 1980). In a recent structure-function study of the MIN (Raczkowski and Sherman 1983), most Y cells were found to have class I morphology. Others located medially possessed flat, fusiform somata but resembled class I cells in their vertically oriented bitufted dendrites. Their soma shape may thus reflect an extreme adaptation to the geometry of the MIN (Meyer and Albus 1981).

The MIN receives an input not only from large axons but also from fine axons (Mason and Robson 1979; Guillery et al. 1980), which form an extension of the fine population in laminae C and C1 (Mason and Robson 1979). Rowe and Dreher (1982) estimate that up to 50% of retinal ganglion cells providing the input to the MIN are of the W-type; they closely resemble in soma size, dendritic morphology and axonal caliber those medium-sized cells which provide the predominant retinal input to the parvocellular C laminae (Leventhal 1982). According to Guillery et al. (1980), fine diameter axons which innervate the MIN terminate preferentially in its most dorsal and medial parts, near the border with the RRZ of the pulvinar (see section I.B.2). However, W-cells provide an input to all layers of the MIN (Guillery et al. 1980; Rowe and Dreher 1982), and W-cells

have been recorded distant from the RRZ/MIN border (Dreher and Sefton, 1979; Raczkowski and Sherman, 1985).

Both 'concentric' (phasic and tonic) and 'non-concentric' W-cells have been encountered in MIN (Dreher and Sefton, 1979). Concentric W-cells fail to respond to large stimuli moving rapidly (above 100 /sec) through their receptive fields. They respond with a modulated discharge to drifting gratings but their temporal resolution would seem to be lower than that of W-cells in the main layers (Dreher and Sefton, 1979). Mason (1981) and Raczkowski and Sherman (1985) have confirmed that a minority of encountered cells in the MIN have W-type receptive fields.

X cells (Dreher and Sefton, 1977; 1979; Mason, 1975) and class 2 cells (Meyer and Albus, 1981b; Raczkowski and Sherman, 1985) are encountered exclusively and in small numbers at the lateral margin of the MIN near its border with the main layers of the dLGN. Some of these cells may have been located in the dLGN proper since lamina C and the MIN are difficult to differentiate in Nissl material (Meyer and Albus, 1981b). Indeed Mason (1978), following Guillery (1970), has considered this border region to be the medial limb of lamina C representing the area of nasotemporal overlap. However, class 2 cells are also encountered in dorsal parts of the MIN where the separation from the dLGN is much clearer. The exclusive location of X-cells in this border region may explain why no Y-cells were labelled following HRP injections into the MIN (Rowe and Dreher, 1982); both Sur and Sherman (1982a) and Bowling and Michael (1984) observed that some X OT axons sparsely innervate the MIN. X-cells in the MIN have been identified on the basis of response properties used to classify X-cells in the main layers except that the most stringent tests for linearity of spatial summation have not been carried out (Mason, 1975; Dreher and Sefton, 1979). Dreher and Sefton (1979) report a small number of cells in the MIN with a mixture of X- and Y-receptive field properties.

1.5. THE LATERAL POSTERIOR (LP)-PULVINAR COMPLEX

The LP-pulvinar complex comprises a large nuclear group in the thalamus located medial to the MIN. It has recently been subdivided medio-laterally into a number of zones (Updyke 1977, Graybiel and Berson 1980) each of which contains a separate representation of the visual field (Raczkowski and Rosenquist 1983). The tecto-recipient zone (Graybiel and Berson 1980) is the most medial of the visually responsive regions of the LP-pulvinar complex. Adjacent and lateral to the tecto-recipient zone is the cortico-recipient zone (Graybiel and Berson 1980) which receives afferents from area 17, area 18 and area 19 in topographic register (Updyke 1977). The posterior nucleus is located ventrally within the cortico-recipient zone, adjacent and medial to the MIN. The pulvinar is situated adjacent and lateral to the cortico-recipient zone and dorsal to the MIN. It receives input from area 19 and the pretectum.

The LP-pulvinar complex receives a topographically organized retinal projection confined to a narrow strip, the retinal recipient zone (RRZ), which comprises the lateral portion of the pulvinar and, ventrally, the lateral part of the cortico-recipient zone including the uppermost portion of the posterior nucleus (Berson and Jones 1977, Berson and Graybiel 1978, Itoh et al. 1979, Kawamura et al. 1979, Leventhal et al. 1980). The input to the RRZ is mediated by fine axons (Guillery et al. 1980) and arises from medium-sized retinal ganglion cells (Kawamura et al. 1979, Leventhal et al. 1980), which have a dendritic field size and morphology similar to that of cells providing the predominant input to the parvocellular C-lamina (Leventhal et al. 1980). Given the close apposition of the RRZ to the dLGN (at some points it is contiguous with the MIN) and its relay function (see Chapter 2), it may be more properly considered as part of the dLGN complex (Mason, 1978, Guillery et al. 1980). Guillery et al. (1980) use the term 'geniculate wing' to refer to a region which comprises the RRZ and a narrow strip extending ventrally from the RRZ to the OT, which is innervated by fine fibres. Many authors, however, consider this narrow region to be part of the

MIN; it contains small cells, whereas the RRZ contains larger, medium-sized neurones and is indistinguishable from the more medial parts of the lateral posterior pulvinar complex (Berman and Jones, 1977). The majority of neurones recorded in the RRZ have properties characteristic of W-cells, though a substantial proportion of Y-cells and a small number of X-cells are also encountered (Mason, 1981). W-cells in the RRZ have large receptive fields and respond poorly to velocities above 50°/sec.

CHAPTER 2

THALAMIC INPUT TO AREA 18: A COMPARISON WITH AREA 17

2.1: Functional Type Of Thalamic Input To Area 17 And Area 18

2.2: Laminar Distribution Of Thalamic Afferents In Area 17 And Area 18

2.1. FUNCTIONAL TYPE OF THALAMIC INPUT TO AREA 17 AND AREA 18

As described in the preceding chapter, the vast majority of cells in the visual thalamus receive their retinal input selectively from either X-, Y- or W-cells. Spatial and temporal integration of excitatory retinal inputs in the thalamus and their modulation by inhibitory circuits leads to differences between thalamic X-, Y- and W-cells and their retinal counterparts. In addition, evidence is beginning to emerge for a certain amount of variation at the post-retinal level in response properties of X-, Y- and W-cells which is related to their location in different nuclei of the thalamus, in different layers of the laminated dLGN or even within the depth of a single layer in that nucleus. Some of the differences in response properties among cells of the same type may be correlated with differences in underlying morphology. There is now substantial evidence from anatomical and physiological sources for quantitative differences in the contribution of different thalamic nuclei of different layers of the laminated dLGN and of different functional types in the thalamus to the subcortical input to areas 17 and 18.

2.1.1. Anatomical Studies

(a) Projections From The Dorsal Lateral Geniculate Nucleus

The *dorsal laminae* of the dLGN project to areas 17 and 18 to the exclusion of other visual areas. The most substantial projection from the A-laminae (70-80% of cells; Lin and Sherman, 1978; Geisert, 1980) is to area 17, which in turn depends most heavily for its thalamic input on the dorsal layers of dLGN; they contribute 94% of the thalamic input to area 17 (Hollander and Vanegas, 1977). Compared with area 17, area 18 receives a relatively weaker projection from the A-laminae (10-15% of cells; Lin and Sherman, 1978; Geisert, 1980) which contributes 47% of its thalamic input (Hollander and Vanegas, 1977). Birnbacher

and Albus (1987) conclude that the projection from the A-laminae to area 17 is five times greater than that to area 18. At least some regions of area 18 receive a stronger projection from lamina A1 than from lamina A (Hollander and Vanegas 1977, Geisert 1980, 1987). The greatest concentration of area 18-projecting cells in the dorsal layers is found in the ventral part of lamina A1 (Geisert 1987).

Compared with area 17, area 18 is relatively more dependent on *lamina* C for its thalamic input. lamina C contributes 20% of the input to area 18, but only 4% of the input to area 17 (Hollander and Vanegas 1977). As described in Chapter 1, W cells located ventrally in lamina A1 and in lamina C can be distinguished physiologically from their counterparts in lamina A and the dorsal part of A1 (Stanford 1981, Fitzpatrick and Lehmkuhle 1984). According to Geisert (1980), 70% of cells in the C laminae project to area 17 and 30% to area 18. Bullier et al. (1984a) and Birnbacher and Albus (1987) also conclude that the projections from the C laminae to areas 17 and 18 are comparably strong.

The *parvocellular layers* contribute no more than 5% of the input to areas 17 and 18, the projection to area 17 being slightly the more substantial (Hollander and Vanegas 1977).

Considered together, neuroanatomical studies which have employed retrograde degeneration (Gatey and Powell 1967), anterograde degeneration (Wilson and Cragg 1967, Niimi and Sprague 1970, Rossignol and Colonnier 1971) and more recently retrograde axonal transport of HRP (Maciewicz 1975, LeVay and Ferster 1977, Hollander and Vanegas 1977, Leventhal 1979, Geisert 1980) and combined anterograde and retrograde transport of HRP (Ferster and LeVay 1978) have provided the following details on the projections of the dLGN to areas 17 and 18: medium-sized cells in the A-laminae project via medium sized axons substantially and almost exclusively to area 17; areas 17 and 18 also receive a projection via large-calibre axons from large cells in the A-laminae and lamina C and a relatively sparse input via fine axons from small cells in the C laminae.

A consideration of the morphology of physiologically identified geniculate cells (Friedlander et al. 1979, 1981; Stanford et al. 1981, 1983), and the cortical projections of geniculate neurones identified on the basis of their entire dendritic morphology (Meyer and Albus 1981b), yields more precise information on the proportions to areas 17 and 18 of different functional types in the dLGN. Area 18 receives a dominant input from class 1 (Y) neurones and a weak input from class 2 cells, while area 17 receives a relatively more substantial input from class 2 than from class 1 cells. Class 3 (X) and class 4 (W) cells provide only a small proportion of the input to area 17 and area 18. Class 1 cells contribute a high proportion of the input to area 18 from both the A lamina (90–95%) and the C lamina (74%), while class 2 cells comprise no more than 10% of the input to area 18 from the dorsal or ventral layers. In contrast, a substantial proportion of the input to area 17 from both the A- and C laminae (74% and 63% respectively) derives from class 2 cells. Class 1 cells comprise only 12–20% of the input from the A lamina and 10% of the input from the C lamina to area 17.

Since most if not all class 2 cells are relay cells, and the majority are of the X-type, area 17 must receive a projection from both X- and Y-cells. The predominant input to area 18 derives from Y cells. Since some class 2 cells are Y cells, it is impossible to determine with certainty the physiological identity of the residual input to area 18 from the A lamina. However, the soma size distribution of class 2 cells projecting to areas 17 and 18 is similar (Meyer and Albus 1981b) and thus at least some class 2 cells projecting to area 18 are likely to be X-cells. Compared with class 1 cells, class 2 cells provide a relatively higher proportion of the input to callosal than to acallosal regions of area 18, which might suggest that the geniculate X-cell input to area 18 is concentrated near its border with area 17. However, the change in relative numbers of class 1 and 2 cells projecting to areas 17 and 18 is not strictly related to that border as defined by physiological or cytoarchitectonic criteria, and geniculate class 2 cells provide a significant input to regions of area 18 distant from its border with area 17. In addition, a small proportion of the input to area 18 from the A-lamina derives from class 3 (X)

cells. Physiologically identified X-axons have been seen to arborize in and to either side of the 17/18 border region (Freund et al. 1985a; Humphrey et al. 1985b), and a lamina-C cell displaying linear spatial summation has been shown to project exclusively to area 18 (Humphrey et al. 1985b).

If class 2 cells in A-laminae project mainly to area 17, and some of those which project to area 18 are X-cells, then the smaller class 2 Y-cells must project almost exclusively to area 17. Thus the Y input from dLGN to area 18 derives from class 1 cells, whereas area 17 receives a mixed Y projection from class 1 and class 2 cells. The demonstration (Humphrey et al. 1985a) that Y-cells in the A laminae which project to area 18 have on average significantly larger somata than those which project to area 17 is consistent with this interpretation.

Class 4 W-cells provide a significant proportion of the input from the C-laminae to areas 17 and 18. With increasing eccentricity the proportion of the input to area 18 from class 4 cells increases, and that from class 1 and class 2 cells decreases.

Since Gatey and Powell (1967) it has been recognised that some cells in the dLGN project to both areas 17 and 18 via axons that branch. However, there is still considerable dispute concerning the proportions of geniculate cells that project to both cortical areas via branching axons. It is clear from the above arguments that the vast majority of cells in the A-laminae which send an axon to both areas 17 and 18 must be class 1 Y-cells. On the basis of physiological evidence Stone and Dreher (1973) concluded that most or all Y-cells in the dorsal layers project to both areas via branching axons. In contrast LeVay and Ferster (1977) found few cells in the A laminae labelled after injections of HRP into area 18 and concluded that only a negligible proportion of Y-cells in the A laminae could send bifurcating axons to both areas 17 and 18. However, other authors (Lin and Sherman 1979; Geisert 1980) reported a much more substantial input to area 18 from the A laminae, and thus the low proportion of labelled cells found by LeVay and Ferster (1977) may reflect small injections of HRP. Geisert (1980) estimated that 10% of cells in the A-laminae project to both areas 17 and 18. If it

is assumed that Y-cells comprise one third to one half of cells in A-laminae (LeVay and Ferster, 1977; Friedlander et al., 1979, 1981), then a fifth to a third of Y-cells in A-laminae project to both areas 17 and 18. Since few Y-cells are likely to be interneurones (Friedlander et al., 1981; Bullier et al., 1984a) report that 12–21% of cells in the A-laminae that project to areas 17 and 18 do so via branching axons is in general agreement with this interpretation. On the other hand, Birnbacher and Albus (1987) insist that the proportion of projection neurones in the A-laminae which send axons to areas 17 and 18 is much lower than this (3%). On the basis of this estimate, no more than about 10% of Y-cells in the A-laminae could send bifurcating axons to areas 17 and 18. Humphrey et al. (1985b) have directly confirmed the existence of axons from Y-cells in the A-laminae that branch to innervate areas 17 and 18, although the majority of their sample arborized in one of the two areas. It is unclear to what extent the input from the A-laminae to area 18 is shared by area 17. Geisert (1980) concluded that 90% of area 18-projecting cells in the dorsal layers also project to area 17, while Bullier et al. (1984a) estimated that only 50% do so. More recently, Birnbacher and Albus (1987) have reported a much lower proportion (18%) of area 18-projecting cells in the A-laminae with an input to area 17.

Estimates of the degree of divergence in the projection from the C-laminae to areas 17 and 18 also vary widely. Geisert (1980) concluded that 50% of cells in the C-laminae project to areas 17 and 18 via bifurcating axons, while Bullier et al. (1984a) estimated that only about 20% do so. Birnbacher and Albus (1987) have recently reported a slightly lower proportion (17%) of cells with bifurcating axons in the projection from the C-laminae to areas 17 and 18. These authors also conclude that only 32% of neurones involved in the projection from the C-laminae to area 18 also project to area 17, an estimate which contrasts markedly with that (83%) of Geisert (1980). Of four axons of lamina-C Y cells recovered by Humphrey et al. (1985b), two branched to innervate areas 17 and 18 and two arborized exclusively in area 18.

Bunhacher and Albus (1987) argue convincingly that the discrepancies in the reported proportions of neurones with branching axons in the projection from the A- and C-laminae to areas 17 and 18 can be attributed almost entirely to differences in the location of sites for the injection of retrograde tracers in the different studies. They claim that in Geisert's (1980) study injections aimed at area 18 were actually located at the transition zone between areas 17 and 18, and that in Bullier et al.'s (1984a) study the location of injection sites close to the area 17–18 border resulted in false double labelling of projection neurones. Thus it would seem that only a small proportion of projection cells in the dLGN have bifurcating axons which innervate both areas 17 and 18.

(b) Projections From The Medial Interlaminar Nucleus

The MIN contributes approximately 2% of the thalamic input to area 18, the proportion of input from the MIN increasing with eccentricity (Hollander and Vanegas 1977; Leventhal et al. 1980). The dominant input from the MIN to area 18 originates in large cells (Garey and Powell 1967; Macchiavello 1977; LeVay and Ferster 1979; Hollander and Vanegas 1977; Leventhal and Keens 1978*a*) with class 1 morphology (Mever and Albus 1981*b*), and is mediated by large-calibre axons (Wilson and Cragg 1967; Nunn and Sprague 1970; Burrows and Hayhow 1971; Humphrey et al. 1985*b*) have described the axonal arborizations in area 18 of a physiologically identified Y axon arising from a class 1 cell in the MIN. Some of the many small cells in the MIN (Kratz et al. 1978*a*) also project to area 18 (Leventhal and Keens 1978*a*). Though these may be W-cells, it should be emphasized that a minority of Y-cells recovered in the structure–function analysis of Raczkowski and Sherman (1987) also had small fusiform somata. The proportion of the input to area 18 from small cells in the MIN increases with eccentricity (Mever and Albus 1981*b*). Class 2 cells comprise a small proportion of the input from the MIN to callosal area 18 (Mever and Albus 1981*b*). At least some of these are likely to be X-cells, since both class 2 cells and X-cells in the MIN are located exclusively near its medial border with the laminated part of the dLGN.

A projection to area 17 from the MIN was identified by Forster and LeVay (1978), Leventhal (1979), Geisert (1980), Numi et al. (1981), Bullier et al. (1984a) and Birnbacher and Albus (1987), but not by Rosenquist et al. (1974), Hollander and Vanegas (1977) or Kennedy and Baleydier (1977). Leventhal (1979), using highly localized injections of HRP into area 17, demonstrated that small numbers of large and small MIN cells terminate there. Birnbacher and Albus (1987) estimate that the projection from the MIN to area 18 is more than three times as large as that to area 17.

Geisert (1980) found both small and large double-labelled cells in the MIN after injections into area 17 and area 18, and thus it is likely that both W and Y cells project to areas 17 and 18 via axons that branch. Bullier et al. (1984a) and Birnbacher and Albus (1987) agree that the projections from the MIN and C laminae comprise a comparable proportion of cells with bifurcating axons which supply both areas 17 and 18. Only 1–2% of cells in the MIN which project to area 18 also send an axon to area 17 (Birnbacher and Albus, 1987).

(c) Projections From The Lateral-Posterior Pulvinar Complex

The most substantial projection to areas 17 and 18 from the LP pulvinar complex derives from the cortical recipient zone (Graybiel and Berson, 1980; Hughes, 1980; Miller et al., 1980), in which the majority of neurones respond preferentially to moving stimuli and are direction-sensitive (Mason, 1981).

According to Leventhal et al. (1981), the retinal recipient zone (RRZ) of the pulvinar projects neither to area 17 nor to area 18. However, Hollander and Vanegas (1977) report a projection to area 18 from a sheet of white matter which separates the LGNd from the LP-pulvinar complex, and massive injections of HRP into the area 17–18 border region (Hughes, 1980) labelled a small number of cells in the RRZ. A projection to area 18 from the RRZ of the pulvinar has been confirmed by Meyer and Albus (1981b). The majority of cells in the RRZ, including those that project to extrastriate visual areas 19 and the lateral suprasylvian area

are as small as those in the parvocellular C-laminae (Leventhal et al. 1980). The projection to area 18 arises from larger cells with class 2 morphology (Meyer and Albus 1981b). Thus, to be speculative, these may be Y- or even X-cells, while W-cells in the RRZ (Mason 1981) may project to other extrastriate visual areas.

There is a sparse projection to area 18 from the lateral posterior nucleus (Hollander and Vanegas 1977, Meyer and Albus 1981b), which arises from neurones with a dendritic morphology and branching pattern similar to that of class 1 cells in the dLGN, but with a larger soma (Meyer and Albus 1981b).

2.1.2. Electrophysiological Studies

Anatomical evidence for a differential thalamic input to areas 17 and 18 has largely been confirmed by electrophysiological studies (Stone and Dreher 1973, Singer et al. 1972, Tretter et al. 1975, Henry et al. 1974, Bullier and Henry 1979b, Dreher et al. 1980, Harvey, Postma, Martin and Whittenridge 1984) which take advantage of the differences in conduction velocity of X-, Y- and W-axons to identify afferents to different cortical areas.

X-cells project almost exclusively to area 17, which also receives an input from Y- and W-cells. Before there was evidence that W-cells relay through dLGN it was believed (Stone and Dreher 1973, Singer et al. 1972) that X-cells provided the dominant input to area 17. However, if the most slowly conducting axons arriving in the striate cortex are interpreted as arising from W-cells, there is substantial agreement between studies that area 17 receives its predominant input from both X- and Y-afferents, and contains a similar proportion of X- and Y-driven cells. The input from W-cells is rather less substantial (approximately 20% of thalamic input to area 17).

The thalamic input to area 18 derives almost exclusively from Y-cells (Stone and Dreher 1973, Tretter et al. 1975, Harvey, Postma, Dreher et al. 1980). The CSD analysis of Mitzdorf and Singer (1978) revealed that the input to area 18

is initiated by one group of homogeneously fast-conducting afferents which are conspicuously faster than the fastest input to area 17. This probably reflects the preponderant input to area 18 from the MIN, which contributes only a small proportion of the input to area 17. The axons of Y-cells in the MIN are faster and more homogeneous in conduction velocity than their counterparts in the laminated part of the dLGN (Kratz et al., 1978b; Dreher and Sefton, 1979). In addition, the dominant input to area 18 from the laminated part of the dLGN arises from cells with the fastest axonal conduction velocity (class 1 Y-cells), which provide a low proportion of the input to area 17. Thus, one would expect the latency of the dominant excitatory synaptic activity revealed by CSD to be significantly shorter in area 18 than in area 17, even though area 18 does not receive an exclusive input from a subgroup of Y-cells. Humphrey et al. (1985b) have confirmed that, despite considerable overlap, Y-axons innervating area 18 have on average significantly faster conduction velocities than those that innervate area 17.

Estimates of the proportion of area 18 cells which receive input from X-cells range from 4–16%. However, some of the slowly conducting afferents reaching area 18 may arise from W-cells since the separation between X- and W-cells on the basis of axonal conduction velocity is not as reliable as that between X- and Y-cells. That the W-cell input to area 18 has not been convincingly demonstrated in electrophysiological studies may reflect the fact that the bulk of the W-cell projection to cortex arrives in the superficial layers (see section 2.2.1), which are more prone to damage, and whose resident cells may be underrepresented in physiological studies. Of course, a similar argument would apply to W-cell projections to area 17. Notwithstanding the claim (Dreher et al., 1980) that the superficial layers of area 18 are more difficult to record from than those of area 17, it is difficult to offer an explanation for the difference in the strength of the W-cell input to areas 17 and 18 revealed by electrical stimulation experiments but not anticipated from anatomical work.

2.2. LAMINAR DISTRIBUTION OF THALAMIC AFFERENTS IN AREA 17 AND AREA 18

Knowledge of the exact localisation of thalamic afferent terminals is central to an understanding of the internal circuitry of areas 17 and 18. The laminar terminations of afferents from cells located in different nuclei of the thalamus or at different depths in the dLGN are now well-documented.

The characteristic pattern of lamination of the visual cortex observed in Nissl stained sections reflects the size, density and distribution of pyramidal and non-pyramidal cells. Non-pyramidal cells can be subdivided into three groups (spinous, sparsely spinous and aspinous stellate cells: Gatey 1971, LeVay 1973) within which there is enormous heterogeneity (Peters and Regidor 1981).

2.2.1. Lamination Of Area 17

The commonly accepted cortical lamination scheme for area 17 is based upon six principal layers arranged parallel to the cortical surface and labelled I-VI (O'Leary 1941, Otsuka and Hassler 1962). The most superficial layer, layer I, is narrow and contains glial and non-spiny stellate cells. The composite layer II/III is a broad band composed principally of small pyramidal and non-spiny stellate cells. The division between these two superficial layers is difficult to discern, but the average size of resident pyramidal cells increases with cortical depth. According to the scheme of O'Leary (1941), a line of large pyramids marks the border between layers III and IV. Layer IV is composed principally of stellate cells and is unique in containing the spinous variety. It is divided into upper and lower sublaminae with respect to cell size, packing density and predominant cell type. The subdivisions IVA/IVB (O'Leary 1941) and IVa/b/c (Otsuka and Hassler 1962) are equivalent (Lund et al. 1979, Humphrey et al. 1985a). Layer IVA consists of rather loosely packed, small-to-medium sized pyramidal neurones, and (predominantly spinous) stellate cells. Layer IVB contains more tightly packed

small stellate cells and a small proportion of pyramidal cells. The cells in layer V are rather sparsely distributed. Layer VA is a narrow sublamina of small and medium-sized pyramidal cells, while layer VB contains the largest pyramidal cells in the striate cortex, interspersed with a larger number of small pyramids. The tops of the somas of large pyramids in layer V marks its border with layer VA. Pyramidal cells are the predominant cell type in layer VI, where they have a distinctly tiered organization.

2.2.2. Termination Of Thalamic Afferents In Area 17

Extracellular tracing studies (LeVay and Gilbert, 1976; Rosenquist et al., 1974; Leventhal, 1979a) demonstrated a dense band of projection from the A-laminae to layer IV and the III/IV border region, a weaker projection to layer VI, and a small but significant projection to lower layer III.

The projection from the A-laminae to layer IVA and the III/IV border region originates in large cells (Leventhal, 1979a) and is mediated by fast-conducting (Mitzdorf and Singer, 1978a), large (presumed class 1) axons (Ferster and LeVay, 1978a). The input to layer IVB arises from small to-medium sized cells (Leventhal, 1979a) and is mediated by more slowly conducting (Mitzdorf and Singer, 1978a), medium-sized (presumed class 2) axons (Ferster and LeVay, 1978a). The conclusion (Ferster and LeVay, 1978; Leventhal, 1979a) that Y-cells terminate in layer IVA, and X-cells in layer IVB rests on the assumption that class 1 cells are Y-cells and class 2 cells are X-cells. However, some Y-cells have class 2 morphology (Friedlander et al., 1981), and thus the larger caliber class 2 axons terminating in layer IVB may arise from Y-cells. On the other hand, Bullier and Henry (1979a) report that the termination of medium-sized axons in layer IV is not restricted to IVB but extends somewhat into layer IVA, and that the terminals from large and medium-sized axons overlap to some extent in the middle of layer IV. Using intracellular injection of HRP into a small sample physiologically identified geniculate axons, Gilbert and Wiesel (1979) reported confirmation of the sublaminar segregation of

X- and Y-afferents in layer IV. However, more extensive studies (Freund et al. 1985a; Humphrey et al. 1985a) have demonstrated substantial overlap in layer IV of terminals of physiologically identified X- and Y-axons. The terminal fields of X-cells are either confined predominantly to layer IVA and the III/IV border region or to layer IVB, or they are distributed throughout layer IV and the III/IV border region. Y-axons terminate predominantly in layer IVA and lower layer III (Freund et al. 1985a; Humphrey et al. 1985a), though some also arborize in layer IVB (Humphrey et al. 1985a). Interestingly, the sublaminar projections of X- and Y-cells in layer IV are related to the location of parent somata within the depth of the A-laminae (Humphrey et al. 1985a). Briefly, the initial view that afferents from X- and Y-cells are segregated respectively into upper and lower parts of layer IV holds only for X-cells in the central third and Y-cells in the outer thirds of the A-laminae.

Geniculate input to layer VI is concentrated dorsally and arises from medium and large cells of the A-laminae (Leventhal 1979) via collaterals of medium and large axons which innervate layer IV (Berster and LeVay 1978). Physiologically identified axons of X- and Y-cells projecting to layer IV have been seen to innervate layer VI, where their terminal fields overlapped substantially (Humphrey et al. 1985a).

The C-laminae project to lower layer III, the III/IV and IV/V border regions and to the superficial part of layer I (LeVay and Gilbert 1976). The small cells of parvocellular C-laminae project via axon collaterals principally to layer I, less substantially to lower layer III, and weakly to the IV/V border region (Berster and LeVay 1978; Leventhal 1979). Small cells in lamina C project to the IV/V border region, while larger cells project to the III/IV border region and upper layer IV (Leventhal 1979).

According to Leventhal (1979), the projection from large cells in the MIN arrives at the III/IV border region and in upper layer IV, while small MIN cells project to layer I.

Thus the evidence to date has provided the following details on the laminar terminations in area 17 of X- Y- and W-afferents: axon terminals from W-cells in the parvocellular C-laminae and from small (W or Y) cells in the MIN arrive in the superficial part of layer I immediately below the limiting membrane. Lower layer I and layer II do not receive thalamic afferents. Lower layer III receives an input from X- and Y-cells of the A-laminae with the projection from Y-cells rising higher than that from X-cells (Humphrey et al. 1985a) and from the W-cells of the parvocellular C-laminae which project to layer I. Upper layer IV and the III/IV border region receives a substantial projection from Y-cells in the A-laminae (lamina C) and the MIN and from X-cells in the A-laminae. The predominant input to layer IVB arises from X-cells in A-laminae, though some A-lamina Y-cells have axons that terminate there. The projection to the IV/V border region from W-cells in the magno- and parvocellular C-laminae partially overlaps the X-cell projection to layer IVB. Axons of some X- and Y-cells which project to layer IV sparsely innervate layer V. X- and Y-cells in the A-laminae project to layer VI, where their axon terminal fields overlap considerably. The input to layer VI is relatively weak compared with that to layer IV, and is concentrated dorsally within the layer.

The amplification of the Y- relative to the X-pathway which begins in the dLGN and MIN (see Chapter 1) is intensified in the cortex. In area 17 Y-axons have more extensive arborisations and make more synapses per bouton than X-axons (Gilbert and Wiesel 1979; Martin and Whitteridge 1984; Freund et al. 1985a; Humphrey et al. 1985a). Notwithstanding the relative difficulty in electrically activating X- compared with Y-fibres (for example: Hoffmann et al. 1972; Stone and Dreher, 1973; Martin and Whitteridge, 1984), this would explain why a similar proportion of X- and Y-driven cells have been recorded in area 17, although there are approximately twice as many X- than Y-cells in the dorsal layers of the dLGN (Friedlander et al. 1981).

2.2.3. Lamination Of Area 18

The cytoarchitecture of area 18 is well-documented (Otsuka and Hassler 1962, Sanides and Hoffmann 1969, Garey 1971, Harvey Pena Humphrey et al 1975). Immediately beneath layer I lies a zone composed principally of small pyramidal cells. This superficial zone was designated layer II by Otsuka and Hassler (1962) and Garey (1971), though Harvey (Pena) preferred the term layer II IIIa in order to convey the difficulty in distinguishing the border between layers II and III. Compared with area 17, the most striking cytoarchitectonic feature of area 18 is that layer III is relatively wide and layer IV correspondingly narrow. Layer III has been divided into two sublayers (Otsuka and Hassler, 1962, Harvey Pena). Layer IIIa consists mainly of small and medium-sized pyramidal cells, while layer IIIb contains, in addition, a scattering of large pyramidal cells. The lower aspect of layer III is situated about half way through the thickness of the cortex and is marked by occasional large pyramidal cells. These occur less frequently than the analogous border pyramids in area 17. In area 18, large loosely-packed pyramidal cells are most prevalent approximately 200μm above the border with layer IV. As in area 17, layer IV is composed of two sublayers. Layer IVB is conspicuous by its relatively small, moderately-packed somata. It is similar to layer IVB in area 17, but contains more medium sized cells and is not as densely-packed. The border between layer IVA and IVB is difficult to discern and involves a gradual transition from the smaller cells in layer IVB to the medium and large, more loosely-packed cells in layer IVA. The increase in cell size continues dorsally within layer IVA. Spiny stellates, which in area 17 are found exclusively in layer IV, are absent from layer IV in area 18. Layer V occupies approximately the same position in area 18 as it does in area 17, but is slightly wider. It is sparsely filled with large pyramidal neurones. The border between layer IVA and V occurs at the level of the apices of the most superficial pyramidal cells comprising layer V. An equivalent to layer VA in area 17 is not apparent in area 18. Layer VI is more densely packed than layer V and is composed chiefly of medium-sized pyramidal cells.

2.2.1. Termination Of Thalamic Afferents In Area 18

The A-lamminae project relatively heavily to layer IV and the III/IV border region (LeVay and Gilbert 1976, Harvey 1980a, Miller et al 1980) and less substantially to layer VI (LeVay and Gilbert 1976, Miller et al 1980). The above authors concluded that axons of cells in A-lamminae terminate throughout layer IV and rise only a short distance (100μm) into layer III. However, according to Humphrey et al (1985b) the terminal fields of axons from Y-cells in the A-lamminae largely avoid layer IVB, but densely innervate layer IVA and the lower 400μm of layer IIIB. The input to layer III is more substantial and rises higher in area 18 than in area 17.

The C-lamminae project relatively heavily to layer IV and less substantially to layer I (LeVay and Gilbert 1976, Miller et al 1980). The axons of Y-cells in lamina C like those of their counterparts in the A-lamminae, arborize densely in layer IVA and lower layer III, but only sparsely innervate layer IVB (Humphrey et al. 1985b). Thus, the primary input from the C-lamminae to layer IVB may arise from W-cells. Axons from Y-cells in the C-lamminae which innervate layer IV also provide a weak input to layers I and VI (Humphrey et al. 1985b). However, the thalamic input to layer VI is considerably weaker in area 18 than in area 17 (Rossignol and Colonnier 1971, Rosenquist et al. 1974, LeVay and Gilbert 1976, Humphrey et al. 1985b).

The projection to area 18 from the MIN arrives in layer IV (Rosenquist et al 1974). An axon of a Y-cell in the MIN has been seen to arborize extensively throughout layer IV, and the lower 400-600μm of layer III, and to sparsely innervate layers V and VI (Humphrey et al. 1985b). The thalamic Y afferents to area 18 recovered by Freund et al (1985a) densely innervated layer IVA, but also provided substantial input to layer IVB. These afferents may have arisen from Y-cells in the MIN or, alternatively, some Y-cells in the dLGN may also have axons which arborize throughout layer IV in area 18.

In accordance with anatomy, the prominent input to area 18 arrives in layer IV

and the input to layer VI is less prominent than in area 17 (Mitzdorf and Singer, 1978). The input to layer I is as insignificant as in area 17.

The lateral spread of Y-afferents in area 18 is 2–3 times larger than in area 17 (Humphrey et al., 1985a,b). Conversely, small HRP injections into layer IV of area 18 (Geisert, 1985) label cells occupying a more extensive region of the dLGN than do comparable injections in area 17 (Leventhal, 1979).

CHAPTER 3

INTRODUCTION

3.1: Previous Comparisons Of Area 17 And Area 18

3.2: Relative Preference And Directional Tuning For Oriented And Textured Stimuli In Area 17 And Area 18 Cells

3.3: Modulatory Influence Of A Synchronously Moving Textured Field On The Responses Of Cells In Area 17 And Area 18

3.1. PREVIOUS COMPARISONS OF AREA 17 AND AREA 18

The pioneering studies of Hubel and Wiesel (1962, 1965) provided the first comparisons of neuronal organization in areas 17 and 18. Compared with geniculate cells (Hubel and Wiesel 1961), the most striking feature of cortical cells was their selectivity for the orientation of light–dark contours in appropriate regions of the visual field. Hubel and Wiesel (1962, 1965) identified three major cell types which, in order to make explicit their hierarchical model of visual processing, they termed simple, complex and hypercomplex. When mapped with small stationary spots of light, the receptive fields of simple cells could be partitioned into at least two adjacent, parallel ON- and OFF-zones, each of which was supposedly due to excitatory convergence from a number of on- or off-centre geniculate cells with receptive fields arranged in a row. Simple cells also resembled geniculate cells in showing summation within and antagonism between receptive field subregions. Cells for which one of these requirements was not fulfilled were classified as complex. Only rarely could separate ON- and OFF-subregions be demonstrated in complex cell receptive fields, and for these (non-uniform complex) cells the principles of summation and antagonism did not hold. Hubel and Wiesel (1962) thought that complex-cell receptive fields could best be accounted for by excitatory convergence from a number of simple cells with identical receptive field axis orientation. Except for their specificity for stimulus length, hypercomplex cells resembled complex cells from which they were thought to derive their excitatory input. In support of their hierarchical model, Hubel and Wiesel (1962) found that in area 17, complex cells were prevalent in the superficial and deep layers, simple cells in layer IV, which was recognized as the major terminal zone of geniculate afferents. The absence of hypercomplex cells in area 17 and of simple cells in area 18 led Hubel and Wiesel (1962, 1965) to conclude that the two cortical areas process information serially, with area 18 receiving its most important input from area 17. Although reciprocal connections were demonstrated between areas 17 and 18 (Wilson 1968), Gilbert and Kelly (1975) found a relatively weak projection from area 18 to area 17, in

line with the hierarchical scheme of Hubel and Wiesel (1962, 1965).

More recently, comparably strong reciprocal connections have been demonstrated between areas 17 and 18 (Bullier et al., 1984b; Symonds and Rosenquist, 1984a) which also receive a similarly high proportion of cells with monosynaptic thalamic input (Singer et al., 1975; Trotter et al., 1977). Moreover, the receptive field properties of area 18 cells are relatively unaffected by ablation or cooling of area 17 (Donaldson and Nash, 1975b; Dreher and Cottee, 1975; Sherk, 1978). The above observations suggest that, contrary to Hubel and Wiesel (1962, 1965), areas 17 and 18 are primary visual areas which process information largely in parallel — a conclusion strengthened by comparisons of the neuronal organization in the two areas. Thus, although a number of different procedures have been employed to classify cells, it is now generally agreed that areas 17 and 18 contain similar cell types (Singer et al., 1975; Trotter et al., 1977; Hammond and Andrews, 1978; Harvey, 1980a; Ferster, 1981; Orban and Kennedy, 1981). The most widely used alternative to the classification scheme of Hubel and Wiesel (1962) is that proposed by Henry (1977) and Henry et al. (1978b) and modified by Orban and Kennedy (1981). A common feature of these rather similar schemes is that, among cells with overlapping ON- and OFF-receptive field subregions mapped with stationary flash-presented stimuli, B-cells are distinguished from C-cells by their sharply-peaking histogram profiles in response to a bar moving across the receptive field. Similarly, among cells with either a single ON- or OFF-receptive field zone or a number of non-overlapping ON- and OFF-subregions, bar motion evokes a sharply-peaking response in S-cells, but a sustained response across the entire receptive field in A-cells. The proportions of these cell types are similar in areas 17 and 18, with S-cells predominating in both areas (Henry et al., 1979; Bullier and Henry, 1979a; Harvey, 1980a; Orban and Kennedy, 1981; Martin and Whitteridge, 1984), and, contrary to Hubel and Wiesel (1965), simple cells are common in area 18 (Ferster, 1981). The laminar distribution of different cell types is similar in areas 17 and 18 (Gilbert, 1977; Leventhal and Hirsch, 1978; Henry et al., 1979; Bullier and Henry, 1979a; Harvey, 1980a; Ferster, 1981; Orban and Kennedy, 1981; Ferster

and Lindstrom, 1983; Martin and Whitteridge, 1984), the distribution of complex or C-cells peaks in layer V and in the superficial layers, while simple or S-cells dominate in layers IV and VI. In both areas, S-cells also dominate in layers II and III (Henry et al., 1979; Bullier and Henry, 1979; Harvey, 1980a; Orban and Kennedy, 1981; Martin and Whitteridge, 1984). Further, the association between cell type and synaptic distance from the thalamus is similar in the two areas. Most S-cells receive monosynaptic thalamic input, while the majority of C-cells are indirectly driven by thalamic afferents (Henry et al., 1979; Bullier and Henry, 1979a,b; Harvey, 1980a; Martin and Whitteridge, 1984). These results are broadly congruent with those of Singer et al. (1977) and Trotter et al. (1975), who compared the afferent connectivity of areas 17 and 18, but classified cells only on the basis of responses to stationary stimuli. Finally, different cell types show comparable differences in response properties in the two areas (Henry et al., 1978b, 1979; Harvey, 1980a; Orban and Kennedy, 1981; Orban et al., 1981b). Thus, C-cells have higher spontaneous activity than S- or B-cells, which have low or absent resting discharge. S-cells are more often monocularly driven than C- or A-cells; they contain the highest proportion of direction-selective cells and, together with B-cells, have the narrowest directional tuning (measured qualitatively). The major difference between the two areas are that area 18 cells have larger receptive fields (Hubel and Wiesel, 1962, 1965), prefer lower spatial frequencies (Movshon et al., 1978a) and respond to higher stimulus velocities (Orban et al., 1981a).

3.2. RELATIVE PREFERENCE AND DIRECTIONAL TUNING FOR ORIENTED AND TEXTURED STIMULI IN AREA 17 AND AREA 18 CELLS

Previous comparisons of response properties of cells in the two areas have been made using oriented stimuli in isolation, but it is clear that the texture of objects plays a fundamental role in visual perception (Gibson, 1950, 1966; MacKay, 1957;

1965). For example, field gradients of texture velocity provide important clues to the speed and direction of self-motion through a textured environment and either as a consequence of self-motion or of real movement, objects are commonly perceived against contoured or textured backgrounds.

In this laboratory visual texture has been used extensively in area 17, both as a stimulus in its own right and as a background against which to present conventional oriented stimuli (Hammond and MacKay, 1975, 1977, 1981b; Hammond, 1978a, 1981a,b; Hammond and Smith, 1983, 1984; Hammond et al., 1986). Thus, in view of the reported similarities in neuronal organization of areas 17 and 18, it was of interest to compare the response properties of cells in the two areas using textured stimuli, particularly since area 18 is thought to be involved in visual movement perception.

Hammond and MacKay (1975, 1977) found that in striate cortex, motion of a field of static visual noise drove only complex cells, which by implication could not receive their sole input from simple cells, as postulated by Hubel and Wiesel (1962). Hammond and Mackay (1977) found excellent texture response in a few cells recorded incidentally from area 18, but quantitative studies of noise sensitivity in this area are limited in number, and are not directly comparable with previous work in area 17. Dinse and von Seelen (1981b) reported that area 18 cells gave little or no response to motion of a field of Gaussian noise, but used a noise process with inappropriate spatial frequency characteristics for area 18 cells. A few authors have reported sensitivity of area 18 cells to motion of various types of random pattern, which are qualitatively and quantitatively different from the type of visual noise used by Hammond and Mackay (1975, 1977); they comprise a random square pattern (Orban et al., 1975; Orban and Callens, 1977a,b), multiple spot patterns (Gibson et al., 1978; Hoffmann et al., 1984), and Julesz noise (Schoppmann, 1981). Recently, in the superior colliculus responsiveness to motion of a field of visual noise and directional tuning for that stimulus depend critically on the type of noise process used (Fromel, 1986a). Further, even allow

ing for the relatively large receptive fields of area 18 cells, the size of the elements in the patterns used by Orban and Callens (1977a,b: 1 × 1°) Gibson et al. (1978, 0.5–7.5° dia.) and Hoffmann et al. (1984: 1.5° dia.) contrasts markedly with the average grain size (4.4′) in the noise used by Hammond and MacKay (1975, 1977). In the studies of Orban et al. (1977), Orban and Callens (1977a,b) and Gibson et al. (1978), the large pattern elements presumably reflect at least in part the peripheral (10–50° eccentricity) and hence large, receptive fields of recorded units. This represents a further difference between studies of noise sensitivity in the two cortical areas for Hammond and MacKay (1975, 1977) recorded from cells in the central projection of area 17.

A major point of interest is whether the differential responsiveness of simple and complex cells to motion of a field of visual noise observed in area 17 (Hammond and MacKay 1975, 1977) also obtains in area 18. A plausible explanation for the noise insensitivity of simple cells in area 17 is that most show linear spatial summation (Movshon et al. 1978a; Andrews and Pollen 1979; Kulikowski and Bishop, 1981; Dean and Tolhurst, 1983) for motion of visual noise causes little or no nett change of flux across the receptive field. However, it is generally assumed that area 18 cells summate non-linearly, since the predominant thalamic input to this area derives from Y-cells (Stone and Dreher 1973; Tretter et al., 1975; Dreher et al., 1980; Harvey, 1980a,b) which show non-linear spatial summation (Enroth-Cugell and Robson, 1966; Hochstein and Shapley, 1976a,b). Moreover, Y-cells in lamina C show a more pronounced non-linear receptive field component than do their counterparts in the A-laminae (Frascella and Lehmkuhle 1984), and area 18 depends more heavily on lamina C for its thalamic input than does area 17 (Hollander and Vanegas, 1977). Indeed, there is now substantial evidence that, to a large extent, different types of Y-cell project to areas 17 and 18. According to Birnbacher and Albus (1987), only a small proportion of the thalamic input to area 18 is shared by area 17, and geniculate cells which project to area 18 are concentrated in lamina C and the ventral part of lamina A1 (Geisert, 1985). Most of these must be Y-cells, given the insubstantial X-input to area 18, and Y-cells

located in lamina C and ventrally in lamina A1 have lower spatial resolution and higher temporal resolution than other Y-cells in the dLGN (Movshon, 1981). Y-cells in the MIN have larger receptive fields than their counterparts in the dLGN (Kratz et al., 1978). Dreher and Sefton, 1979), and the MIN contributes a large proportion of the thalamic input to area 18 but projects insubstantially to area 17 (Hollander and Vanegas, 1977; Leventhal, 1979; Gerfen, 1984; Leventhal et al., 1980; Meyer and Albus, 1981b; Numi et al., 1981; Burnacher and Albus, 1987). The variation in the physiological properties of Y-cells as a function of location in the thalamus and (presumably) cortical projection site must be associated, at least to some extent, with differences in underlying morphology, since the Y-input to area 18 derives from class 1 cells, while area 17 receives an input from both class 1 and class 2 Y-cells (Meyer and Albus, 1981b). It is known that X-, Y- and W-cells respond to moving visual noise (Mason, 1978a,b; 1981; Hoffmann et al., 1981; Ahmed and Hammond, 1983; Hoffmann and Stone, 1985), although some retinal W-cells with non-concentric receptive fields (Hoffmann and Stone, 1985) and a minority of cells in the visual thalamus (Mason, 1978a,b) fail to respond to whole-field noise motion. However, there have been no *quantitative* comparisons at the geniculate level of the strength of response to noise field motion of the different functional classes in the dLGN, or of the different types of Y-cell in the thalamus. In the retina, magnitude of response to motion of a field of visual noise depends on the antagonistic interaction between receptive field centre and surround (Ahmed and Hammond, 1983), and X-cells have more potent surrounds than Y-cells (Ikeda and Wright, 1972b; Cleland et al., 1973; Hammond, 1974; Hamasaki and Cohen, 1977; Bullier and Norton, 1979b). The suppressive effects of the receptive field surround are more potent in the dLGN than in the retina (Hubel and Wiesel, 1961; Singer et al., 1972; Hammond, 1973; Maffei and Fiorentini, 1973; Lee et al., 1981; Cleland and Lee, 1985), and there is some evidence that the difference in surround strength of X- and Y-cells is accentuated at the geniculate level (Lee et al., 1981; Troy, 1983a; Cleland and Lee, 1985). Pertinently, Mason (1978a,b) reported in some 20% of cells in the thalamus, suppression of spontaneous activity by whole-field noise motion (sometimes with superimposed

response peaks), which was associated with the presence of a strong "suppressive field". Thus, one might anticipate that Y-cells, which provide the predominant input to area 18, respond more vigorously to moving noise than X-cells, which project almost exclusively to area 17. To take the argument a step further, the evidence cited above implies that Y-cells projecting to area 18 have on average larger receptive field centres than do those which project to area 17, and in the dLGN, the potency of the suppressive effects of the receptive field surround is inversely correlated with the size of the receptive field centre (Hammond, 1973; Bullier and Norton, 1979a,b). Differences in the noise sensitivity of the Y-cell input to areas 17 and 18 might also be expected on morphological grounds. Y-cells with class 2 morphology presumably participate in the classic triadic complexes in the dLGN and, as a result of potent feed-forward inhibition from retinal ganglion cells, may show relatively weak responses to noise-field motion.

Most previous studies in which random patterns have been used as stimuli in area 18 have not addressed the issue of the noise sensitivity of different cell types. Hoffmann et al.'s (1984) study was restricted to area 18 cells which responded well to a random spot pattern, while Schoppmann (1981) reported noise sensitivity in layer V cells in areas 17 and 18 which project to the nucleus of the optic tract (NOT). Neither Hoffmann et al. (1984), whose data were obtained from awake cats, nor Schoppmann (1981) classified cells according to conventional criteria. Gibson et al. (1978) reported that in area 18, most cortico-pontine cells (but none of the cells in a comparison group) responded better to a multiple spot pattern than to oriented stimuli. However, they attempted to classify cells only as complex or hypercomplex. Since, even in the comparison group, no cell was reported to be unresponsive to a moving multiple spot pattern, and since it is now established that simple cells are common (Ferster, 1981) and S-cells predominant (Harvey, 1980a; Orban and Kennedy, 1981) in area 18, it is possible that some of Gibson et al.'s (1978) complex cells had simple or S-type receptive fields and responded to random pattern motion. The closest parallel with the studies of Hammond and MacKay (1975, 1977) is that of Orban and Callens (1977a), who

reported that the ratio of response to a moving random square pattern and to a drifting grating was much higher for complex than for simple cells, implying that at least some 'simple' cells responded to the random square pattern. On the other hand, Orban and Callens (1977a) did not use stationary stimuli to classify cells and thus could not distinguish simple cells from B-cells which, in area 17, respond (weakly) to moving noise (Hammond and Smith, 1983, 1984). Even conventional complex cells in area 17 do not show uniformly strong sensitivity to noise. Deep-layer complex cells are strongly sensitive to noise, while superficial-layer complex cells show enormous heterogeneity in noise sensitivity (Hammond and MacKay, 1977; Hammond, 1978c; Hammond and Smith, 1983, 1984). In the studies of Orban et al. (1975) and Orban and Callens (1977a), there is little evidence of variation in the magnitude of relative response of complex cells to motion of a random square pattern, apart from a slight tendency for cells with shorter response latencies to be less sensitive to random pattern motion. The results of Gibson et al. (1978) do suggest some degree of heterogeneity in complex-cell response to a multiple spot pattern but, as mentioned above, some of the cells classified as complex may have been simple or S-cells. Moreover, previous assessments of relative response to a random pattern in area 18 (Orban et al., 1975; Orban and Callens, 1977a; Gibson et al., 1978) may have been confounded by differences in preferred direction and velocity tuning for motion of oriented and textured stimuli, as have been found in area 17 complex cells (Hammond, 1978c, 1981a,b; Hammond and Reck, 1980b; Hammond and Smith, 1981). directional tuning for bar motion is invariant with velocity, while tuning for visual noise is typically unimodal at low velocity, but becomes progressively more bimodal as velocity is increased, with the trough of depressed response corresponding to directions optimal for a bar. Preferred and upper cut-off velocity are characteristically higher for noise than for bar motion. It can not be assumed, however, that such differences also obtain in area 18, particularly since it has been claimed (Movshon et al., 1980) that in area 17, the bimodality of tuning and higher velocity preference for noise is artefactual.

Movshon et al. (1980) speculate that in area 17, bimodal tuning for noise at high velocities is a reflection of a cell's sensitivity to the vectorial component of texture velocity in the preferred direction for a moving bar. Since the vector of velocity in this direction is lower than the velocity of noise motion to either side, this hypothesis predicts the higher upper cut-off velocity for noise. Hammond and Smith (1983) have outlined a number of reasons for rejecting this hypothesis. Thus, some cells remain unimodally tuned at all velocities of noise motion to which they respond. In bimodally tuned cells, the two lobes of tuning can be asymmetrically displaced in terms of direction about the peak in tuning for a bar, or of unequal strength. Finally, bimodal tuning can develop below the preferred velocity for noise or for bar motion. Nevertheless, the hypothesis of Movshon et al. (1980) is consistent with the influence of velocity on directional tuning for noise in many area 17 cells, particularly those with velocity low-pass (VLP) functions for bar motion (Orban et al., 1981a). These cells are predominant in area 17 subserving central vision, but virtually absent in area 18. Conversely, velocity tuned (VT) and velocity high pass (VHP) cells are common in area 18, but rare in area 17 (Orban et al., 1981a). According to the hypothesis of Movshon et al. (1980), VHP cells should remain unimodally tuned for noise at all velocities, with similar preferred directions for noise and bar motion, while VT cells should develop bimodal tuning for noise only at high velocities when the response to bar motion is on the decline. There has been no previous quantitative study of the directional tuning of area 18 cells for motion of oriented and textured stimuli over a range of velocities, but isolated observations are not inconsistent with Movshon et al.'s (1980) hypothesis. Thus, Orban and Callens (1977b) claimed that in VHP cells in area 18, velocity-response functions are similar for motion of a slit and a random square pattern, and they did not report differences in preferred directions for the two stimuli; their illustrated VHP cell was unimodally tuned for a random square pattern moving at the preferred velocity for that stimulus. Gibson et al. (1978) also illustrated an area 18 cell with unimodal tuning for a multiple spot pattern moving at high velocity; they mentioned that in some cells, preferred direction for a grating was different from that for the random pattern, but bimodality of

tuning was not reported. Hoffmann et al. (1984) described area 18 cells with VT and VHP functions for a random pattern moving in the preferred direction for that stimulus, but gave no information concerning the velocity at which directional tuning curves were compiled. The above observations, in conjunction with the theoretical considerations of Movshon et al. (1980), warranted a quantitative investigation of the influence of velocity on directional tuning for noise in area 18 cells, quite apart from the intrinsic interest in deriving such data for comparisons with results from area 17.

One argument used by Hammond and Smith (1983) in rejecting Movshon et al.'s (1980) explanation of bimodality of tuning for noise was that some area 17 complex cells with unimodal tuning for noise, or bimodal tuning with lobes of unequal strength, show broader tuning for motion of a long bar on the flank closest to the preferred direction for noise (Hammond, 1978c; Hammond and Smith, 1983). Thus in these cells, asymmetry of bar tuning presumably reflects stimulation of the directional mechanism by a moving bar (Hammond, 1978c). Consistent with this hypothesis, Bishop et al. (1980) described an asymmetrically tuned hypercomplex cell in area 17, in which tuning for noise was bimodal with lobes of unequal strength, and the preferred direction for a moving spot, which presumably would provide relatively stronger drive to the directional mechanism than a moving bar, shifted away from the preferred direction for bar motion towards the major lobe of tuning for noise. Against this, however, it has been claimed that in both simple and complex cells, preferred direction (but not broadness of tuning) is independent of stimulus length (Henry et al., 1974a,b). This is consistent with Movshon et al.'s (1980) hypothesis, which implies that each cell has a single preferred direction which is invariant for all stimuli. In view of the apparent discrepancy between these results, which have an important bearing on conflicting explanations of directional tuning for visual noise (Hammond and Reck, 1980b; Hammond and Smith, 1983; cf. Movshon et al., 1980), it was of interest to compare the directional tuning of a few cells in areas 17 and 18 for motion of noise, bar and single spot stimuli.

The major objective of the present study, however, was to provide direct, quantitative comparisons of the noise sensitivity and directional tuning for oriented and textured stimuli of cells in areas 17 and 18 with receptive fields at comparable eccentricities, using identical animal preparation, experimental procedure and visual stimulation. Receptive fields were classified as S-, C-, B- and A-type according to identical criteria in each area (Orban and Kennedy, 1981), and superficial-layer C-cells were distinguished from deep-layer C-cells (see Chapter 5). Directional tuning for noise and bar motion was compared over a range of velocities, in order to make an accurate assessment of relative preference for the two stimuli, and to compare in cells with different velocity-response functions for bar motion the influence of velocity on directional tuning for noise. Such directional tuning curves additionally provided quantitative comparisons in each cell of noise sensitivity, broadness of bar tuning, direction sensitivity and level of spontaneous activity. These data, together with information on receptive field width and ocular dominance (Hubel and Wiesel, 1962) of each cell, allowed comparisons with the results of Hammond and Smith (1983, 1984) who found that in area 17, strongly noise-sensitive, deep-layer complex cells had relatively large receptive fields, high spontaneous activity and broad directional tuning, and were almost exclusively direction-selective and binocularly-driven, while the variation in noise sensitivity of superficial-layer complex cells was associated with receptive field size, level of spontaneous activity, directional sensitivity and tuning for bar motion.

The experimental procedure additionally yielded the first quantitative comparisons of directional tuning for bar motion of S-, C-, B- and A-cells in areas 17 and 18, which could be related to previous qualitative and quantitative results. The observations of Harvey (1980a) suggest that broadness of tuning of each of these cell types is comparable in areas 17 and 18. However, according to the qualitative data of Orban and Kennedy (1981) (and see Orban, 1984), S-cells in area 17 have sharper tuning than their counterparts in area 18, though in each area, C-cells have comparable tuning, which is broader than that of S- or B-cells. On the other hand, in the only previous quantitative study of directional tuning

in area 18. Hammond and Andrews (1978) found that complex type 1 and type 2 cells (equated respectively with area 17 simple and complex cells) did not differ substantially in directional tuning.

3.3. MODULATORY INFLUENCE OF A SYNCHRONOUSLY MOVING TEXTURED FIELD ON THE RESPONSES OF CELLS IN AREA 17 AND AREA 18

In area 17, synchronous motion of a textured background can modulate the responses of both simple and complex cells to moving foreground bar stimuli (Hammond and MacKay, 1977, 1981b; Hammond and Smith, 1982, 1983, 1984; Hammond et al., 1986). The sensitivity of complex cells in area 17 to relative motion between oriented stimuli and textured backgrounds has been investigated extensively (Hammond and Smith, 1982, 1984; Hammond et al., 1986). In the present study, comparable investigations in area 18 were eschewed in favour of extensive quantitative comparisons in noise-sensitive cells of directional tuning for noise and bar motion over a range of velocities. However, the modulatory influence of a synchronously-moving visual noise background on bar-evoked responses was investigated in all noise-insensitive cells in area 18. Though not driven by motion of visual noise alone, simple cells in area 17 show suppression of responses to moving optimally-oriented foreground bars by whole-field background noise motion (Hammond and MacKay, 1981b). It could not be assumed that comparable results would obtain in area 18, for it has been reported that simple cells in this area, unlike their counterparts in area 17 (Hoffmann and von Seelen, 1978), do not show a decrease in signal-to-noise ratio for the detection of a moving bar when its *superimposed* noise field is moved in-phase, rather than held stationary (Dinse and von Seelen, 1981b). However, the noise process used by Dinse and von Seelen (1981b) provided little or no excitatory drive to area 18 cells when moved alone. Thus it was anticipated that synchronous motion of a background of visual noise

with appropriate spatial frequency characteristics might suppress the bar-evoked responses of some area 18 cells which were not driven by noise motion alone. On the other hand, such suppression may not be specific to simple cells. Of the few superficial-layer complex and B-cells in area 17 with poor noise sensitivity described by Hammond and Smith (1984), some showed suppression of responses to moving bar stimuli by synchronous background motion. In others, however, a synchronously-moving noise background was uninfluential on bar-evoked responses and, even in simple cells, the influence of synchronous background motion is often weak or negligible (Hammond and Mackay, 1981b). These results imply a dichotomy within cells of the same class in terms of suceptibility to the suppressive influence of synchronous background motion, which would have important functional implications. However, in area 17, the modulatory influence of background noise motion has been investigated almost exclusively using comparison bars of optimal length and width (Hammond and Mackay, 1981b; Hammond and Smith, 1984). Pertinently, Hammond and Mackay (1981b) reported that in area 17 simple cells, the suppressive influence of moving noise backgrounds was more extensive lengthwise than widthwise across the receptive field, and that its potency declined with increasing distance from the centre. Thus, there is good reason to suspect that when the parameters of a bar stimulus are set optimally for each cell, those textural elements responsible for the greatest amount of response attenuation are obscured and that, partly for this reason, the observed magnitude of suppression might be critically dependent on the length of the bar used to obtain a criterion response. Indeed, Hammond and MacKay (1981b) mentioned briefly that the suppressive influence of synchronous background motion could be enhanced by decreasing the length of the comparison bar, though they attributed this effect to the weaker criterion responses produced by shorter bars. It is difficult to establish whether bar length or strength of criterion response is the critical factor in determining the observed magnitude of suppression in simple cells, which show substantial length summation. However, susceptibility to the suppressive influences of synchronous background motion is not specific to simple cells (Hammond and Smith, 1984), and some complex (Ferster, 1981) or C-cells (Harvey, 1980a,b) in

area 18, like their counterparts in area 17 (Palmer and Rosenquist, 1974; Gilbert, 1977; Hammond and Ahmed, 1985), show restricted length summation. In these cells it may be possible to investigate the magnitude of suppression by synchronous background motion as a function of bar length over a wide range, independent of the strength of the criterion response. By the same token, Hammond and MacKay (1981b) described the modulatory influence of background motion on responses of simple cells to bars moving only in the preferred direction, and indeed area 17 simple cells are predominantly direction-selective. Hammond and Smith (1984) mentioned that in some superficial-layer complex and B-cells, background motion was suppressive of responses to bar motion in both preferred and opposite directions, but gave no indication of the magnitude of suppression in each direction. Background motion might conceivably suppress by a constant amount or by a constant percentage the response to a bar of fixed length moving in preferred and opposite directions. Alternatively, the magnitude of suppression in the two directions might be independent. Thus, in area 18 cells of all classes which were insensitive to noise motion alone, the modulatory influence of synchronous, in-phase background noise motion was investigated on responses to optimally-oriented bars of fixed width but variable length, moving at the preferred velocity in both directions along the axis orthogonal to bar orientation. This procedure additionally allowed comparisons of response modulation in preferred and opposite directions with the length-response characteristics for each direction of motion.

A further reason for exploring the modulatory influence of synchronous background motion on response to bars of variable length was related to the intention of investigating moving noise suppression as a function of stimulus velocity. Previous studies of the modulatory influence of synchronous background motion on responses of cells in the cat visual cortex (Hammond and Mackay, 1981b; Hammond and Smith, 1982, 1984; von Grunau and Frost, 1983; Hammond et al., 1986) have used extensively a paradigm in which a foreground stimulus moved in the preferred direction at near-optimum velocity, while the background was moved at different velocities relative to it, in-phase and in antiphase. A complementary

approach, which might be expected to provide insight into the properties of the suppressive input, is to compare as a function of stimulus velocity, the magnitude of suppression of response to a foreground bar by synchronous background noise motion, with both stimuli moving in the preferred direction for a bar, with the same phase, amplitude and velocity. For reliable quantitative comparisons of moving noise suppression as a function of velocity, it was necessary to use a comparison bar for which suppression was substantial at the preferred velocity, but which would be expected to provide consistent drive, and thus yield an adequate criterion response, throughout most of the effective velocity range. Synchronous motion of the noise background might conceivably produce a linear subtractive change in cell firing rate, and thus percent suppression would be maximum for the velocity at which the bar evoked the weakest criterion response(s). Alternatively, synchronous background motion might induce a divisive-like change in firing rate, in which case percent suppression would remain relatively constant irrespective of the strength of the criterion response, and would thus be invariant with stimulus velocity. A specific reason for investigating the influence of stimulus velocity on magnitude of moving noise suppression stems from reports (Orban et al., 1981a; see discussion in Bishop et al., 1980) that at least in VT cells, percent end-zone inhibition is maximum at the preferred velocity for a bar of optimal length. Percent suppression of bar-evoked responses by moving noise backgrounds might be similarly dependent on velocity, in which case previous studies, where the parameters of the foreground stimulus were set optimally in each cell (Hammond and MacKay, 1981b; von Grunau and Frost, 1983; Hammond and Smith, 1984), may have revealed maximum suppression. On the other hand, it remains to be demonstrated that the velocity-dependence of end-zone inhibition is a general property of end-stopped cells of all velocity types. Thus, one of the important objectives of the present study was to compare directly in end-stopped cells, the magnitude of end-zone inhibition and moving noise suppression as a function of stimulus velocity. Full details of rationale and experimental procedure are given in results (Chapter 7).

CHAPTER 4

METHODS

4.1: Physiological Preparation

4.2: Optics

4.3: Terminal Recording From Chronically Implanted Animals

4.4: Recording

4.5: Experimental Procedure

4.6: Statistics

4.7: Histology

4.1. PHYSIOLOGICAL PREPARATION

Thirty-seven male and female adult cats (mean body weight 2·8kg, range 1·8-3·7kg) were prepared conventionally for acute recording sessions of three to four days duration. For preliminary work in area 17 and initial recordings from area 18, animal preparation and interleaved 12h recording sessions were shared with a colleague recording extracellularly from single units in the dLGN, in the hemisphere contralateral to that in which cortical penetrations were made. Latterly, experiments were carried out independently. This procedure proved more satisfactory in terms of greater cortical stability with time, and more productive with respect to the number of units isolated and successfully recorded from during an experimental run.

A single anæsthetic regime was followed in all experiments. Typically 8-10min were required to induce an adequate level of surgical anæsthesia with 5% halothane (Fluothane, ICI) administered with a Fluotec MK3 (Cyprane) in a 72·5%/27·5% mixture of N_2O/O_2. During the induction period the behavioural state of the animal was closely monitored and any tendency to breath-holding was quickly obviated by means of frequent manual depression of the abdominal cavity. When the animal was deeply anæsthetized, 2-3% halothane in the nitrous oxide/oxygen mixture was supplied by means of a face mask.

Tracheotomy was not performed. Rather, with the aid of a laryngoscope, cats were intubated with an appropriately sized Magill cuffed endotracheal tube (Frankhns) coated with lignocaine antiseptic gel. Tube diameter (typically 4·0mm) was compatible with the animal's weight in order to ensure a good seal within the trachea and reduce the possibility of obtaining a non-veridical reading of end-tidal CO_2. Available tube diameters ranged from 3·0-4·5mm in steps of 0·5mm. Upon introduction of the tube, the cuff was inflated by the application of syringe pressure, and securely clamped.

Intramuscular procaine penicillin (Depocillin, Brocades, 300mg/ml) was administered prophylactically at a non-lethal dose of 0·1ml/kg, directly after intubation and subsequently every 24h. Aspiration ensured that the syringe needle was not located in a blood vessel.

The electrocardiogram (ECG) was recorded differentially across skin electrodes attached to the thorax and abdomen. The signal was amplified by a Devices 3160 amplifier (gain ×100, bandwidth 80–250Hz) with additional amplification between ×2 and ×200. The R-wave was discriminated and heart-rate was monitored aurally over a loudspeaker, and continuously on a Devices MX2 heat-sensitive pen recorder.

Artificial ventilation was necessary in the early stages to stabilise end-tidal CO_2 at physiological levels and later to combat arrest of spontaneous respiration caused by the administration of a muscle relaxant to reduce eye movements. Halothane concentration was reduced to between 1·5 and 2·0%. End-tidal CO_2, monitored breath-by-breath by an infra red medical gas analyser (Beckman LB 2), in conjunction with a continuous write-out on one channel of a Devices M2 heat-sensitive pen recorder, was maintained within the range 3·8–4·0% by adjusting the stroke volume of an artificial respirator (C. F. Palmer), set at a fixed rate of 28 strokes per min. Strict control of end-tidal CO_2 was observed at all times, since hyperventilation leads to EEG spindling, irrespective of behavioural state (Hammond 1978b). During physiological preparation, when concentrations of halothane were high, stroke volume was in the region of 25–30cc per stroke. After discontinuation of surgical anaesthesia an increased value of around 50cc per stroke was typical.

The cat was transferred to a Narishige stereotaxic frame providing minimal obstruction of the visual field. The head was held initially by means of ear bars with well-rounded tips, in conjunction with orbital and palate bars, thus defining a horizontal stereotaxic plane in Horsley-Clarke (H-C) co-ordinates and restraining the head in the correct attitude. The left cephalic vein was cannulated for intravenous infusion (Butterfly 23G, Abbott Laboratories) of gallamine triethiodide

(Flaxedil, May and Baker). An initial infusion of 20mg/kg induced paralysis, and a continuous infusion thereafter of 20mg/h in a 5% dextrose solution (0·8ml/h) maintained eye immobilisation. The immediate effect of the commencement of Flaxedil infusion was invariably an increase in heart-rate, due to release from the depressant effects of halothane, sometimes followed by mild and transitory fibrillation of the heart.

A rectal thermistor probe coated with K-Y lubricating jelly (Johnson and Johnson) was introduced and used to monitor body temperature which was maintained by a homoeothermic blanket control type 8158 (C F Palmer) at a constant 38·5°C.

With the animal securely mounted in the stereotaxic frame, cauterisation along the midline of the scalp and reflexion of the underlying temporalis muscles with a periosteal scraper was undertaken. Two self-tapping stainless steel screws were inserted respectively over the left auditory and right posterior visual cortices to allow differential recording of the surface cortical electroencephalogram (EEG). Occasional bleeding from the spongy bone was successfully overcome by the application of bone wax. The EEG signal was amplified through a Devices 3160 amplifier (gain ×1000, bandpass 0·8–50Hz) and written out on a Devices M2 recorder. All pen chart recordings were retained for subsequent reference. It was occasionally necessary to insert hooks, attached to lead weights, beneath the scalp to prevent skin margins making contact with screw electrodes and thus shorting out the EEG. At this stage the EEG waveform consisted of continuous, large-amplitude slow waves indicative of Stage IV (surgical) anæsthesia (Ikeda and Wright, 1974). A headclamp, rigidly attached to the nasal and frontal bones of the skull by stainless steel screws, provided atraumatic head restraint with no obstruction of the visual field. Ear, orbital and palate bars of the stereotaxic instrument were removed thereafter. In most experiments a small perspex or nylon chamber (base diameter 1cm) was seated in dental acrylic applied to the skull over the left striate and extrastriate visual cortices. Subsequent internal and external application of acrylic around the base of the chamber ensured a secure attachment to the skull.

which was then cleaned with cetrimide. All wound margins were infiltrated with a long-lasting local anæsthetic (Xylocain spray, Astra), typically 6 sprays applied through a metered valve releasing 10mg of lignocaine per spray. A round dental burr (No. 5) was used to make a small craniotomy (3-5mm base diameter) vertically over the left visual cortex and centred on the appropriate H-C co-ordinates (see section 4.4.2.) so as to expose the underlying protective dura. Residual bone chips were removed with a fine dental probe. To prevent drying, the craniotomy was covered with a cotton wool pellet soaked in 0·9% saline. On completion of surgical procedures, the halothane concentration was reduced and, according to the state of the animal as determined by monitoring criteria, was adjusted within the range 0·5-1·0% during the next 1-2h. Because of the slight variation in susceptibility of each animal to anæsthesia, EEG, heart-rate and end-tidal CO_2 were all assessed in relation to the reflex state of the animal *prior* to paralysis, for use as more reliable criteria of adequate anæsthesia *during* paralysis. Despite a reduction in halothane concentration, and presumably because of prolonged exposure to high levels of halothane during surgical preparation, it was not uncommon for the animal, throughout the time taken to prepare the eyes for visual stimulation, to display an EEG waveform typical of Stage IV anæsthesia under which cortical units would be completely undriveable. Ikeda and Wright (1974) report that a 2·2% halothane concentration in 80% N_2O/O_2 is associated with a fall in steady-state blood pressure to a level barely adequate to support retinal circulation, and that even after halothane is discontinued, mean arterial blood pressure remains low for several hours, permanently impairing circulation. Thus during surgical procedures, anæsthetic level was allowed to lighten as far as was consistent with satisfactory monitoring criteria, in order to reduce the possibility of irreversible deterioration of the preparation.

4.2. OPTICS

From induction until transference to the stereotaxic instrument, the cat's eyes were kept closed. Before commencement of surgical procedures, they were washed with warm 0·9% saline. Eyelids and nictitating membranes were retracted with 10% phenylephrine hydrochloride, and pupils were subsequently dilated with 1% atropine sulphate (Mimms, Smith and Nephew). To prevent desiccation of the corneal surface, two-curve neutral contact lenses (Hamblin, base diameter 8·0mm/ peripheral diameter 12·0mm) were applied with wetting solution (Transol, Smith and Nephew). Three pairs of lenses were available with base/peripheral curves 8·0/8·5mm, 8·5/9·0mm, 9·0/9·5mm. The correlation derived by Andrews and Hammond (1970) between corneal radius of curvature and body weight, based on the data of Vakkur et al. (1963) and Vakkur and Bishop (1963), provided an approximate guide to the selection of lenses with appropriate curvature. In addition, gross refractive errors outside the normal range, revealed by subsequent slit retinoscopy (Keeler), confirmed the application of an inappropriate lens. Upon completion of surgical procedures, lenses were removed, rinsed in cold water, dried and re-applied with either phenylephrine hydrochloride or atropine sulphate. Excess fluid around the perimeter of the lens was carefully absorbed. Since in the anæsthetized, immobilised preparation the eyes are focused near infinity, subsequent spherical correction by trial lens spheres was necessary to focus the eyes for a viewing distance of 57cm. The locations of the areae centrales were ophthalmoscopically back-projected (Fernald and Chase, 1971) onto a removable perspex screen positioned immediately in front of the visual display (see 4.3.1).

The retinae were routinely scanned for abnormalities. Inspection of the fundus in one cat revealed a severely abnormal inferior retina of the right eye, possibly due to the development of a cataract. Since, however, the majority of units isolated in previous penetrations had receptive fields in the lower quadrant of the contralateral hemifield representing the superior retina, the experiment was continued. Successfully isolated cells responded briskly to visual stimuli and their receptive fields were all in the lower half of the visual field. In one cat, central retinal degeneration (Bellhorn et al., 1974) was evident, which consisted of a darkened annulus around the perimeter of the area centralis. All successfully

isolated cells had receptive fields near the area centralis projections. In two cats showing a similar retinal abnormality, Mason (1976a) found no cells in the dLGN with receptive fields occupying the central 4° of the visual field. The discrepancy is probably explained by reference to the different types of lesion encountered by the two authors. Bellhorn et al. (1974) report that in cats with small focal lesions, typical of those in Mason's animals, abnormal cone electroretinographic (ERG) responses were observed, together with a certain amount of degeneration peripheral to the lesion. However, in one cat with an elliptical lesion of the area centralis they identified no associated rod or cone ERG abnormalities, and rods and cones immediately outside the lesion area were found to be functionally intact.

Throughout the course of a long, acute experiment it was necessary to check periodically the quality of the optic media. The eyes were irrigated daily with 0·9% saline. Opacity due to corneal clouding, which threatened to result in premature termination of the experiment, was in most instances successfully overcome by irrigation of the eyes with hypertonic (3%) saline and subsequent flushing with warm 0·9% saline. During the later stages of an experiment, however, it was not always possible to reverse pupillary constriction, closing of the eyelids or the reappearance of the nictitating membranes by a simple reapplication of the appropriate pharmacological agent. When deterioration of the optics was more apparent in one of the two eyes, it was permanently occluded and the other eye alone was visually stimulated.

4.3. TERMINAL RECORDING FROM CHRONICALLY IMPLANTED ANIMALS

Some terminal acute experiments were performed on cats which had previously been chronically implanted (Hammond, 1980) with a stainless steel peg for atraumatic head restraint, and a capped nylon chamber positioned symmetrically over the midline above the primary visual cortex. Incorporated within the chamber wall were two gold-plated terminals from teflon-insulated stainless steel wires leading to screw electrodes, driven flush with the cortical surface for differential EEG

recording. Deviations from the routine acute preparation described above consisted of: bipolar EEG recording via existing terminals within the chamber wall; the use of the implanted peg for atraumatic head restraint located in a bridge unique to each implanted cat; the use of an implanted nylon chamber as a reservoir for agar to reduce pulsations (see section 4.4.2.); the selective removal with the hot tip of the cautery unit of certain sections of the implanted chamber to facilitate the enlargement of the craniotomy for recordings from area 18 and the examination of the cortical surface through the dissecting microscope; the placement of microelectrodes with reference to precisely defined penetrations made in recent 'recovery' sessions and with respect to previously determined chamber coordinates; confirmation of previously determined area centralis locations retained on a clear perspex screen which could be slotted in front of the visual display; pre-selection of corrective lenses, with respect to the previously assessed refractive state of the eye, and of neutral contact lenses with appropriate base/peripheral curve.

4.4. RECORDING

4.4.1. Anæsthesia

During the recording stage, a lightly-anæsthetized preparation was used. In preliminary experiments, despite a reduction in halothane concentration at the beginning of the first recording session to a value within the range 0·25–0·75%, the animal remained deeply anæsthetized for several hours. Most units isolated during this period were either undriveable or had weak, inconsistent responses to visual stimuli. Thus, in all but the earliest experiments, halothane supplementation was temporarily withdrawn before initial microelectrode penetrations were made. Used as the sole anæsthetic, nitrous oxide is inadequate for maintaining anæsthesia

during physiological recording in cats (Richards and Webb, 1975, and in this laboratory, Hammond, 1978a,b; R. Mason; C.R. James, unpublished observations), and there is no evidence that Flaxedil potentiates anæsthesia in cats maintained on nitrous oxide/oxygen mixtures alone. Flaxedil infusion together with artificial ventilation at high concentrations of nitrous oxide is associated with a fall in mean arterial blood pressure, but little correlated change in the EEG which would suggest a deepening of anæsthesia (Ikeda and Wright, 1974). Paralysed cats under nitrous oxide alone develop an EEG waveform which in non-paralysed cats is always associated with an unsatisfactory behavioural state (Hammond, 1978b). Thus, despite variability between cats, within a period of 30min to 3h after the discontinuation of halothane supplementation, EEG spindling declined in amplitude and frequency and became interspersed with small-amplitude fast activity. Supplementary halothane (typically 0·2–0·4%) was given at this stage to prevent the appearance of exclusively desynchronized activity in the EEG waveform indicative of arousal (Hammond, 1978a,b). Unless the physiological condition of the animal was extremely unstable, as was sometimes the case during the initial recording session, it was not necessary to increase halothane concentration throughout the duration of an experiment.

4.1.2. Microelectrode Penetrations

Vertical penetrations were made initially in area 17 (H-C co-ordinates: P3·0–6·0, L1·5–2·0) and more extensively in area 18 (P2·0–4·0, L3·0–4·0) within 4mm of the cortical surface (Tusa et al., 1978, 1979). Conservative penetration co-ordinates were chosen to ensure unequivocal recording from each area, while strict adherence to the medial limit for penetrations in area 17 excluded undesirable electrode tracks exclusively within the superficial layers down the medial bank of the lateral gyrus. Although recording site was not routinely verified histologically, occasional terminal histology (see section 4.7.) served to confirm that characteristic electrode penetrations aimed at area 18 were indeed well within that area. In addition,

for all cells recorded in both areas 17 and 18, quantitative data were obtained on velocity sensitivity which, in cortex subserving central and paracentral vision (0–10°), is the most reliable physiological criterion for determining recording site in the vicinity of the area 17–18 border (Orban et al., 1980).

Extracellular recordings were made from single cortical neurones by means of a glass micropipette, pulled to a fine tip, which was then chipped to an external diameter of 1–2μm. Pipettes were filled partly by capillarity with 4M-NaCl and back-filled with the same solution. Air bubbles were removed prior to calibration. The calibrated DC impedance of all viable electrodes ranged from 0·5–1·5MΩ. Under the coarse control of a micromanipulator (Narishige), electrodes were lowered vertically towards the surface of the brain and, under the fine control of a hydraulic microdrive, were usually inserted through stereotaxically defined micropunctures, made with 27-gauge hypodermic needles, in the intact dura. Occasionally, a durotomy was performed, which facilitated the introduction of intact micropipettes and obviated the possibility of damage to the superficial cortical layers by the dural puncture needle. These advantages, however, had to be weighed against the short-term increase in vascular pulsation and long-term impairment of cortical viability associated with removal of the dura. Electrode impedance usually doubled in neural tissue, though a penetration was continued if electrode impedance increased upon entering the cortex, but did not reach twice its calibrated value. A lower impedance than that obtained at calibration was indicative of a shattered tip.

Microelectrodes were initially advanced 250μm. The application of pre-cooled (39°C) 2% immuno-agar (Oxoid) in 0·9% saline effectively sealed the craniotomy, preventing leakage of cerebrospinal fluid and improved recording stability by reducing pulsations. The agar was allowed to completely fill the recording chamber and was covered with low melting point wax to prevent dehydration.

In some experiments the main cause of recording instability was respiratory rather than vascular pulsation. Under surgical anæsthesia, spinal elevation was per-

formed on these animals, which consisted in removal of skin over the spine, insertion of a needle between the 7th and 8th vertebrae and attachment of the thread of the needle to an overlying bridge in order to elevate the animal and so reduce the pressure within the thoracic cavity (E F Evans, P Hammond; personal communication). The partial improvement in recording stability offered by this procedure had to be offset against the increased halothane concentrations necessary for anæsthetic sufficiency during recording sessions.

4.4.3. Recording Equipment

The equipment used to record neuronal activity in area 17 and area 18 will be described separately.

(a) Area 17

For recordings in area 17, signals were fed through a Bak preamplifier with unity gain and negative capacitance neutralisation, subsequently amplified by an Isleworth Electronics A101 preamplifier (filter bandpass 0·2-5kHz), and displayed conventionally on a Tektronix RM565 dual-beam oscilloscope, furnished with an upper beam type 2A63 differential amplifier, and a lower beam type 3A74 four-trace amplifier. A window discriminator allowed separation from the background noise of spikes of different amplitude, the display of which was intensified by Z-modulation.

Discriminated spikes were monitored aurally, either independently of or together with the background noise, and as standard 1μsec pulses were fed to: (i) a Devices MX2 heat-sensitive pen recorder and displayed continuously as firing rate, (ii) electronic counters (Advance TC11A) suitably gated for delay and duration.

Gated discriminated spikes were led to: (i) a Biomac 1000 data retrieval computer (Data Laboratories) for generation of peri-stimulus-time histograms (PSTHs) and directional tuning curves, (ii) a Tektronix D11 storage oscilloscope, and displayed as a dot raster where each dot represented one discriminated spike and each row the response to one stimulus sweep.

(b) Area 18

For recordings from area 18, electrode signals were initially passed through a Neurolog (Digitimer Ltd) unity gain headstage amplifier to a Neurolog NL103 AC preamplifier (×100), filtered by a modified Neurolog NL115 filter module (low frequency cut-off 200Hz, high frequency cut-off 2·5kHz) and displayed on a Tektronix D10 single-beam oscilloscope with supplementary amplification by a Tektronix unit 5A23N. Additional plug-in units included a 4-trace 5A14N amplifier and a dual time-base amplifer 5B12N. Spike discrimination and aural monitoring were as described above for area 17 recordings. Z-modulation was effected by locking in to the chop frequency of the oscilloscope.

Standard pulses were fed to: (i) a Devices MX2 heat-sensitive pen recorder for continuous monitoring of firing rate; (ii) OMB 745 counter-timers gated for delay and duration; (iii) a Neurolog NL750 averager module with a variable sweep-time pre-selected either internally or by means of an external clock control; (iv) a Tektronix R5111 storage oscilloscope, either directly for dot raster generation or indirectly via the NL750 averager for visualization of PSTHs.

4.5. EXPERIMENTAL PROCEDURE

4.5.1. Visual Stimulation

Visual stimuli were generated electronically and displayed on a Hewlett-Packard 1300A display at a viewing distance of 57cm (1cm = 1° visual angle). Average screen luminance of 0·9 log cd/m^2 was midmesopic in conjunction with 5mm artificial pupils (Ahmed et al., 1977), which were aligned centrally over the area centralis. Contrasting stimuli were 0·3 log units brighter or 0·6 log units darker than a background of stationary or moving 'static' visual noise, which was always present so as to prevent adaptational changes. Note that the noise field

was not superimposed on contrast bar stimuli so as to simulate a signal detection task (cf. Hoffmann and von Seelen, 1978; Hoffmann et al., 1980; Dinse and von Seelen, 1981b). Rather, a contrast bar was always clearly visible, obliterating a background of visual noise which, when stationary, caused no obvious response modulation compared with a neutral, homogeneous background of the same average luminance (Ahmed and Hammond, 1984).

The noise background consisted of a square raster of 256 lines × 256 elements (50/50 black and white) in a pseudorandom array, modulated by a special purpose generator (Mackay and Yates, 1975) to produce up to 50 frames/sec. For preliminary experiments in area 17, noise frame size was $10 \times 10^{\circ}$ and the average grain size 4 arc. More extensive recordings from area 18 required an enlargement of both frame and grain size by a factor of 2 to accommodate the poorer spatial resolution in that area (Movshon et al., 1978c). No more than 3 consecutive elements were of the same polarity of contrast. It was possible to change the noise sample in order to control for non-uniformities in grain density. Integrated circuit chips were used to generate simultaneously 2 pseudorandom pulse trains. Control circuitry allowed Z-modulation of the CRT display to be switched electronically from one pulse train to the other or to a black or white signal. This produced a moveable and rotatable 'Figure' of variable shape on a moveable and rotatable 'Ground'. Either could be filled out in black, white or static noise locked to 'Figure' or to 'Ground'. Thus, the 'Figure' or noise background could be moved independently across the screen along an axis orthogonal to bar orientation or synchronously with the same phase, velocity and amplitude of movement. The perimeter of the noise field remained stationary, though its orientation changed, for all directions of motion.

Stimulus sweep was controlled by generators (Ramp Generator G5214, Exact Electronics Inc., or Tektronix Type 162) which produced waveforms of variable type, duration and repetition rate. During the initial search for units, waveform generators were switched to free-run mode to provide uninterrupted linear stimulus

motion across the visual field.

4.5.2. Unit Isolation

Since many cortical cells are silent in the absence of visual stimulation, search stimuli were routinely presented simultaneously to both eyes. Typically, a long bar was moved with a velocity to which most cortical cells would show some sensitivity, either alone or alternately in unison with the background noise field. Direction of motion was varied through 360° in coarse steps of 15–20°. An oriented stimulus in motion was used since not all cortical cells respond to stationary flash-presented stimuli or to moving visual noise. Further, the response to a moving contrast bar is often more distinct over the loudspeaker than the response to a moving noise stimulus, which is capable of exciting a cell throughout the duration of its traverse; the higher firing *frequency* typically induced by a positionally specific stimulus enables an evoked response to be more easily distinguished from the background activity.

A long bar and a large excursion were chosen so as to cover as much as possible of the contralateral hemifield before the precise visual field location for units in a particular penetration had been ascertained. In addition, a number of short hand-held stimuli were used intermittently in an attempt to excite the sophisticated end-stopped cells in the superficial cortical layers. The approximate visual field position of driven, multiunit activity was centred on the texture frame by coarse positioning of the visual display and fine X-Y control of the frame itself. Individual units were isolated with fine, smooth movements of the electrode tip by manipulation of the hydraulic microdrive and occasionally by lateral or medial movements of the micromanipulator. Simultaneously, adjustments were made to the parameters of the search stimulus (such as shape, velocity, direction of motion) which were consistent with an audible increase in firing. In later experiments, the entire noise field was moved alone across the visual field in an effort to selectively isolate cells strongly responsive to moving visual noise. Even when such a

positionally non specific stimulus was used for searching purposes, maximum excursion of movement was retained in view of the report (Orban et al., 1977b) that the response of some cells in area 18 to a global stimulus increases as a function of the amplitude of movement, independent of its velocity or duration.

4.5.3. Mapping Of Receptive Fields

The depth at which isolated single units were encountered and the eccentricity and elevation of their receptive fields was recorded. Ocular dominance (Hubel and Wiesel, 1962) was estimated for a moving contrast bar, and an accurate receptive field map for the dominant eye was plotted onto the perspex screen in front of the visual display.

(a) Primary Borders

The primary borders, which run parallel to the optimum orientation, were defined by the minimum response field method (Barlow et al., 1967). For cells with a pronounced resting discharge, the precise position of the primary borders was invariably more difficult to determine than that of the lateral borders since, in the latter case, final assessment could be made on the basis of several identical trials as the test stimulus oscillated repeatedly across the visual field near the receptive field limits. The relative difficulty in defining receptive field width was more apparent for some cells in area 18 which did not respond to slowly moving stimuli. Manually sweeping a contrast bar across the receptive field evoked a high frequency burst of impulses of short duration. The problem of reliably determining response onset for such cells is obvious. In addition, receptive field width could not be determined quantitatively from PSTHs since apparent receptive field width increases with velocity (Orban et al., 1981a). For these cells, fast oscillatory movements of small amplitude were used to determine the primary borders of the receptive field.

The obvious method of defining receptive field width in bidirectional and direction-biased cells is to determine the onset or potentiation of firing at the proximal edge of the receptive field as a bar stimulus is swept in both directions. This procedure could however result in an underestimate of receptive field width since, although there is considerable overlap, the geometrical position of the field is not identical for different directions of motion (cf. Dinse and von Seelen, 1981a). Thus, in cells which were not direction-selective, receptive fields were mapped for both directions of motion. Since direction sensitivity is a labile property of cortical cells, bar velocity and occasionally bar length were varied in order to establish whether a significant response to motion in the non-preferred direction could be elicited. Any evoked activity was spatially defined and incorporated into the receptive field plot. For cells which responded to bar motion in only one of two directions along a common axis, one of the primary borders was defined by response offset as a long bar moving in the preferred direction left the distal edge of the receptive field.

(b) Lateral Borders

The lateral borders were mapped using the minimum response field method (Barlow et al., 1967). This method seriously underestimated receptive field height yielding, in exceptional cases, a negative value due to the threshold for length summation. Thus, qualitative and quantitative assessments of length summation were routinely carried out in all cells by monitoring spike activity as a short oscillating bar was extended lengthwise symmetrically about the receptive field centre. Accurate location of the field centre itself was determined by moving a short bar of optimum orientation and direction through a number of equally spaced paths through the receptive field orthogonal to its axis. A comparison of receptive field height as determined by each method provided a useful adjunct to cell classification (see Chapters 5 and 7). Each cell was subsequently classified according to receptive field structure and characterized by secondary response properties (see Chapter 5).

4.5.4. Data Collection And Analysis

To enable the generation of PSTHs or directional tuning curves the waveform generators were switched to the triggered mode to initiated a triangular waveform. A reed relay provided alternation between pairs of dissimilar stimuli each of which was moved in both directions along the axis orthogonal to optimum orientation. Data were accumulated virtually simultaneously for the purposes of comparison thus reducing bias due to fluctuation in responsiveness. In order not to confound amplitude and velocity of motion, gate duration was systematically decreased with increasing velocity. This produced aperiodic runs for which stimulus duration decreased with increasing velocity and the pause between forward and reverse sweeps of the same stimulus increased by a corresponding amount. Fig. 4.1 illustrates sweep duration and inter-sweep interval for the range of velocities used. For all but the three slowest speeds, inter-sweep interval exceeded the 500ms necessary for demonstrating responses to high stimulus velocities in area 18 cells (Dinse and von Seelen, 1981a).

(a) Peri-Stimulus-Time Histograms

For the generation of PSTHs to investigate interaction effects (Chapter 7), 16 responses were averaged to motion of a contrast bar against a background of stationary visual noise interleaved with synchronous motion of both stimuli in-phase and at the same velocity. Minimum stimulus excursion was governed by receptive field width and the size of the narrowest bar capable of evoking a consistently good response from a cell: the traverse of the positionally specific stimulus always significantly exceeded minimum response field width. Bar width was set optimally, but parameters such as bar length and velocity were systematically varied (see Chapter 7 for details). Since stimulus excursion always exceeded receptive field width and maximum stimulus sweep time was 1sec, responses to very slow velocities could not be analysed. Adjustment of sweep amplitude for different receptive field widths meant also that the range of velocities tested was not nec-

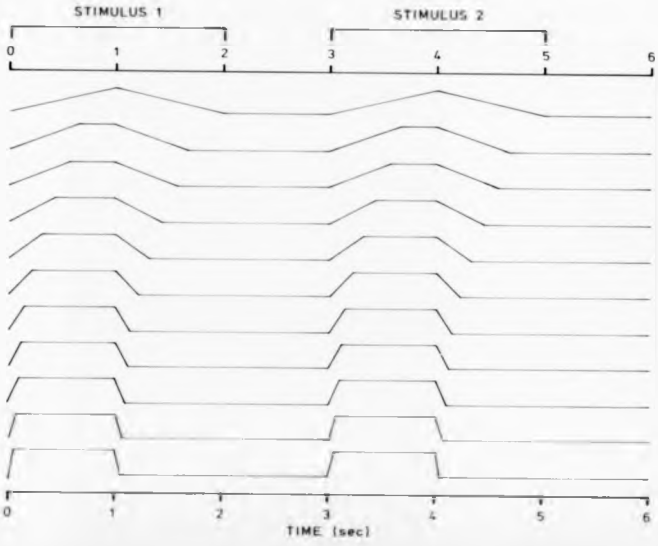

STIMULUS 1
STIMULUS 2
0
1
2
3
4
5
6
TIME (sec)

Fig. 4.1. Stimulus sweep duration and inter-sweep interval for the range of velocities used in the present study. At the lowest velocity, stimulus motion is periodic and consists of a 2sec movement for each of 2 selected stimulus conditions (1sec in each direction), followed by a 1sec pause during which stimuli are switched. With increasing velocity, gate duration is systematically decreased and the pause between forward and reverse sweeps of the same stimulus increases by a corresponding amount.

essarily identical for each unit. The slowest velocity tested was determined by stimulus excursion multiplied by maximum gate duration (1sec). A reduction in gate duration by a constant percentage was matched by increased velocity through 11 pre-selected steps.

When one is measuring response as a function of velocity, the response measure used critically determines the tuning profile one obtains. It is necessary to consider two fundamentally different methods of response evaluation. Time-independent methods such as counting the mean or total number of evoked impulses per stimulus sweep are clearly unsuitable when stimulus duration is being varied. Responses to fast stimulus velocities measured in this way are artefactually low and the velocity response curve almost invariably shows a decline in response with increasing velocity. Conversely, extrapolation from impulses/sweep to impulses/sec biases results in favour of responses to fast stimulus motion and exaggerates response variability. Nevertheless, records of the number of impulses elicited during each stimulus sweep, available from counters with a delay of 50ms and suitably gated for stimulus duration, were retained to provide a measure of sweep-to-sweep variability and to assess whether response differentials were consistent or due to a small number of unrepresentative responses.

A measure of spike frequency, though, gives a more reliable estimate of response to stimulus motion since it eliminates the dependence on response duration which decreases monotonically with velocity over a wide range. Average firing rate is a more difficult measure to evaluate than maximum firing rate since it requires determination of response duration which differs from stimulus duration at fast velocities. According to Orban et al. (1981a) the two measures correlate closely, but average firing frequency depresses response to slow movement, presumably because neurones cannot sustain the same high firing rate for long stimulus durations. Thus, maximum firing rate was used throughout as the primary measure of response. For responses of cells in area 17, PSTHs were generated with a bin-width of 50ms on a Biomac analyser and plotted out using a Bryans 29000

analogue plotter. For recordings from area 18, discriminated spikes were led to a Neurolog NL750 averager and thence to a Tektronix 5111 oscilloscope for visualization of histograms as compiled sweep-by-sweep. Permanent records of complete PSTHs were drawn on a H Instruments PL100 X-Y plotter. All data, together with trigger pulses and stimulus gates, were stored on magnetic tape on a CR3000 Bell and Howell AM/FM cassette recorder. In addition, since for recording the responses of cells in area 18, on-line selection of an appropriate bin-width often proved problematical, all data were subsequently replayed and histograms generated off-line using bin-widths of 40, 21·48 and 10·24ms duration. The longest bin-width was selected by means of an external clock control and only a proportion of the 256 available bins was used. A 21·48ms bin-width was determined by the internal clock of the averager and was equal to the sweep time divided by the total number of bins. Thus, for the generation of a shorter bin-width, a second identical averager was employed with a delay of 3000ms. Each averager was responsible for one half of each complete cycle.

Clearly, the preference for fast velocities and higher velocity cut-off of cells in area 18 necessitates using short bin-widths. According to Shannon's Theorem (see Orban et al., 1981a, p1045), bin-width should always be less than half the minimum response duration. When stimulus velocity is fast, a short bin-width yields a smooth histogram with a well-defined peak. For slow velocities of stimulus motion, however, employing the same bin-width results in an irregular histogram with no discernible peak. Measuring the greatest number of spikes in any one bin, yields an artificially high value for histogram height, while integration over a number of bins centred on the peak would be inappropriate due to the enormous variability between the content of adjacent bins. On the other hand, although a 40ms bin-width produces a smooth histogram for slow velocities of stimulus motion, it is unsuitable when medium and fast velocities are used and response duration is short. The question of bin-width selection is even more important when one wishes to examine response differentials between two stimuli. For reliable comparisons one would like ideally to be able to integrate over a number

of adjacent bins centred on the peak of a smooth histogram. The use of short bin-widths at slow velocities exaggerates differences and yields very erratic results. Yet, for integration purposes, a long bin-width is not permissible over the whole velocity range: at fast velocities, integration period would exceed response duration. Thus, irrespective of stimulus velocity, smooth histograms were generated to assess peak response from the 2 or 3 adjacent bins containing the highest spike count. Thus, the 40ms bin-width gave way to a 21·48ms bin-width only when, with increasing velocity, the integration period exceeded half the response duration. Similarly, a 10·94ms bin-width was used only if response duration was so short as to make integration with a bin-width of 21·48ms duration unsuitable.

For comparison with cells whose responses were analysed from histograms with different bin-widths, results were converted to impulses/sec: $x/(n \times bu)$, where x = number of impulses contained in the peak bin or averaged over a number of bins centred on the peak minus resting discharge, n = number of sweeps, bu = bin-width in sec.

Mean spontaneous firing rate was evaluated from the two periods in the PSTH corresponding to pauses during 1 cycle between movement of each stimulus. The analysis period began 500ms after the cessation of movement and thus increased with increasing stimulus velocity. Spontaneous firing was not calculated from a number of PSTHs representing response to different stimulus velocities (cf. Orban et al., 1981a) and did not provide a constant baseline throughout the velocity range. Rather, evoked discharge was derived from maximum firing rate minus resting discharge assessed at the time each histogram was compiled.

(b) Directional Tuning Curves

Directional tuning curves were generated after a method developed by Hammond (Hammond and Reck, 1980a, Hammond, 1981a). The present study describes data for the alternate motion of a light or dark bar or single spots moving against

a stationary noise background, and motion of the same noise field alone (Chapters 5 and 6). Bar width was set optimally for each cell. Excursion of motion and bar length were set so as to ensure complete coverage of the minimum response field. Pairs of directional tuning curves were compiled for typically 4 successive 'round-the-clock' sequences of directions. Direction, always orthogonal to bar orientation, was advanced sequentially in increments of 10°, by rotating the noise frame symmetrically about the centre of the receptive field every 6sec following forward and reverse sweeps of both stimuli of a pair. The non-randomized sequence of directions has negligible influence on tuning curves for noise and bar motion — the direction of stepping imparts no measurable hysteresis (Hammond and Rock, 1980a; Hammond, 1981a). At the slowest velocity, 1sec motion in each direction was followed by a 1sec pause during which stimuli were switched. With increasing velocity, the duration of each back-and-forth sweep decreased and both the inter-sweep interval and the pause between successive stimulus presentations increased by a corresponding amount. At the end of each 'round-the-clock' sequence, 2 or 3 complete cycles were used to record cell activity in the presence of a stationary noise background. This measure of resting discharge was used subsequently to evaluate evoked activity and to reveal suppression of firing. Impulses elicited by each stimulus for each direction of motion were fed through four gates and gated spikes were accumulated separately in 72 sequential bins of the Biomac 1000 histogram analyzer plus 8 or 12 bins corresponding to resting discharge. Bin advance was controlled externally by pulses delivered 1, 2, 4 and 5sec after the initiation of each cycle. After resetting to the first bin the whole procedure was repeated. Data were unscrambled and plotted by switching the analyser to the four channel mode and outputting channels 1–4 in order, each channel containing counts corresponding to half a complete tuning curve. Calibration of tuning curve height was achieved by the initiation, after the final 'round-the-clock' sequence of a 200Hz calibration signal, which occupied 2 or 3 complete cycles and corresponded to a firing rate of 50 impulses/sec for 4 sequences. Fig. 4.2A shows a representative directional tuning curve as derived on line. For the presentation of results, calibration bars were used to derive an appropriately scaled Y-axis


A
90
260
270
80
90
260
270
80
DIRECTION (deg)
B
DIRECTION OF MOTION
MOVING VISUAL NOISE
MOVING BAR
STIMULUS SEQUENCE
90°+270°
170°+350°
180°+ 0°
260°+ 90°
RESTING DISCHARGE
1
2
3
4
TIME (sec)
0
1
2
3
4
5
6
STIMULUS SWEEP

Fig. 4.2. On-Line Derivation Of Directional Tuning Curves.

A Representative example of a directional tuning curve for motion of a field of visual noise (above) and a contrast bar (below). Each bin represents the summed response of the cell to 4 sweeps of 1 stimulus in a particular direction, commencing at left with an arbitrarily chosen direction of 90° (motion to the right) to 260°, and from 270° (motion to the left) to 80°. The final 3 bins in each presentation are calibration bars representing a mean firing rate of 50 impulses/sec. Broken lines indicate resting discharge averaged over 12 bins (the 3 bins preceding each calibration bar).

B Cell responses registered on a dot raster display during the compilation of a directional tuning curve. Each dot represents a single cell spike. Each row represents the response to visual noise and to a contrast bar moving in the directions shown. Direction stepped in 10° intervals between rows. Each sequence represents responses to noise and bar stimuli moving in forward and reverse directions along a common axis for 18 axes of motion (taken in 2 blocks of 9), followed by 3 cycles of resting discharge followed, after the 4th sequence only, by 3 cycles of calibration (50 impulses/sec.).

representing impulses per sweep, and direction of motion was represented along an uninterrupted X-axis. Continuous records of the short-term temporal pattern of spike firing during consecutive stimulus cycles, and of sequence-to-sequence variability were available from the dot raster display (Fig. 4.2*B*), which was photographed for permanent reference after the compilation of each directional tuning curve, by means of a Shackman Polaroid Camera (Super 7 MKII).

Synchronisation pulses, stimulus gates and cell responses were recorded on magnetic tape for off-line generation of directional tuning curves using the four channels of a CR3000 Bell and Howell cassette recorder. Permanent records of directional tuning curves were plotted after appropriate scaling on a Bryans [illegible] analogue plotter.

Since a positionally specific bar stimulus lies within the receptive field for only part of its sweep, whereas a moving noise background covers the receptive field throughout its motion, counts of impulses/sweep as contained in the bins of directional tuning curves would be expected to impose a bias in favour of the latter stimulus whose magnitude would depend on the relationship between excursion and receptive field width. Such a bias would deflate by a constant amount the response to a bar moving in all directions. However, preferred direction(s) and tuning profile for the noise and bar motion would remain unaltered. In addition, since stimulus excursion was not increased with velocity, bias in favour of moving visual noise would remain constant throughout the velocity range, and velocity preference for the moving bar would not be underrated.

Nevertheless for area 17 cells, information contained in directional tuning curves in the form of cumulative spike totals was supplemented by the off-line generation of PSTHs for each 6sec cycle. For area 18 cells, whose responses were recorded over a wide range of velocities, plotting of peak firing frequency (with integration over the three adjacent bins containing the greatest number of spikes) yielded more realistic directional tuning curves and gave a better indication of the relative velocity preference for bar and noise motion.

4.6. STATISTICS

Statistical comparisons in Chapters 5 and 6 were made using non-parametric statistics (Siegel, 1956), since the assumptions on which parametric significance tests are based were violated in the data (cf. Krauth, 1983).

4.7. HISTOLOGY

In some experiments, the author assisted a colleague (S.R. Deans) in the extracellular iontophoretic ejection of HRP into area 18. Terminal histology on these animals served to identify electrode penetration site. Only details of the HRP protocol relevant to the present study are produced below.

At the end of a penetration, a saline-filled microelectrode was removed and replaced at identical stereotaxic co-ordinates by an HRP-pipette (diameter 10-15μm, impedance 1-2MΩ) containing 10% HRP in a 0.5M KCl buffer solution (pH 7.6), which was lowered to the cortical depth at which the recording penetration had been terminated. HRP was ejected by passing for a period of 30min a positive current of 5μA delivered as 0.5Hz square wave pulses generated by a Devices Mark IV isolated stimulator and triggered by a Wavetek waveform generator. After a survival time of 12-24h during which units were recorded in subsequent penetrations at different co-ordinates, the animal was sacrificed with intravenously administered Nembutal (Abbott Laboratories) and perfused transcardially with 2000ml of warm fixative (1% paraformaldehyde and 1.25% glutaraldehyde in a phosphate buffer, pH 7.4). This was followed by a further 1000ml perfusion of cold (4°C) fixative. Relevant sections of the brain were blocked and stored overnight in the same solution. Before sectioning on the freeze microtome, the tissue was immersed for 24h in 0.2M phosphate buffer (pH 7.4) containing 10%

sucrose. Fifty-micron sections were collected in small (10mm dia.) reaction chambers filled with the same phosphate buffer without sucrose. The reaction procedure followed immediately after sectioning and consisted in pre-incubation for 20min at room temperature with 0·338g Hanker-Yates reagent (sigma (Hanker et al., 1977)), intensified with 1·35g cobalt chloride and 0·9g nickel sulphate, in 225ml 0·1M cacodylate buffer (pH 7·4), and the transference for the same amount of time to a solution of Hanker-Yates reagent to which 4 drops of H_2O_2 were added. The sections were rinsed, wet-mounted through distilled water onto glass slides, air dried for counterstaining with cresyl violet, dehydrated through an ascending series of alcohol solutions, cleared and coverslipped prior to microscopy.

CHAPTER 5

NOISE SENSITIVITY OF CELLS IN AREA 18: A COMPARISON WITH AREA 17

5.1. CELL CLASSIFICATION

5.1.1. Classification Of Visual Cortical Cells

Since Hubel and Wiesel (1962), a variety of cell classification schemes have been employed in visual cortex. It has proved impossible for a consensus to be reached as to the most valid criteria for classifying cortical cells, though few would claim that their classification schemes are completely satisfactory. As described in Chapter 3, Hubel and Wiesel (1962) classified cells according to receptive field structure as revealed primarily by stationary flash-presented stimuli. This is not the complete picture, however, for Hubel and Wiesel (1962) also reported that simple and complex cells differed in their responses to moving stimuli. Simple cells gave a brief, sharply-peaking response to a moving slit, whereas a complex cell gave a sustained response to movement over a much wider region. In fact, Hubel and Wiesel used mainly moving stimuli to classify over half of their simple cells and admitted that many of these may have exhibited more 'complex' properties had they been tested further. This obviously detracts from the hierarchical model of cortical processing proposed by Hubel and Wiesel (1962) as well as diminishing the discriminatory power of their classification scheme. Indeed, the simple cells tested with moving stimuli were presumably unresponsive to stationary flash-presented stimuli and, according to the criteria employed by Hubel and Wiesel (1962), should have been classified as complex. The lack of correlation between classification based on responses to stationary and moving stimuli makes comparisons of studies from different laboratories hazardous, while at the same time pointing clearly to the existence of types intermediate between simple and complex cells. Further, the concept of hierarchical processing within the visual system, so inextricably linked with the classifying scheme of Hubel and Wiesel (1962, 1965) is, at least in its extreme form, no longer tenable (see Introduction and Discussion). By the same token the term 'hypercomplex', which was used by Hubel and Wiesel (1965) to refer to cells with length specificity, is unsuitable for, since

Dreher (1972), hypercomplex cells have been recognized as variants of simple as well as complex cells.

The classification scheme of Hubel and Wiesel implies a correlation between cortical receptive field structure and afferent connectivity, both in terms of synaptic distance from the dLGN and with respect to the input from on- or off-centre geniculate cells. An alternative approach is to classify cortical cells according to the criteria employed in the functional classification of retinal ganglion cells and geniculate neurones, parallel to the on-off-centre dichotomy. Such a classification scheme might be expected at the same time to provide information about the functional type of geniculate input to a cortical cell. An indication of X-input might be linear spatial summation, though it is not at all clear whether non-linearity of spatial summation in the cortex is due to a non-linear input or to a non-linear output of a linear input. Further, since X-cells project almost exclusively to area 17 (see Chapter 2), linearity of spatial summation may not be a particularly useful criterion when applied in other cortical areas. In addition, although spatial summation within receptive field subregions was thought to be one of the cardinal features of simple cells in the striate cortex (Hubel and Wiesel, 1962), quantitative tests show that width summation depends critically on contrast level (Henry et al., 1974a) and that linearity of spatial summation is not an attribute of all area 17 simple cells (Movshon et al., 1978a). Ikeda and Wright (1975) have suggested that cortical cells can be classified as sustained or transient by the criterion used to classify retinal ganglion cells and geniculate neurones. However, the distinction between sustained and transient responses seems to become increasingly blurred along the retino-geniculo-cortical pathway. The sustained component is particularly sensitive to levels of anaesthesia and can easily be overlooked. The most prominent sustained components of cortical cell responses bear only a superficial resemblance to the sustained responses of retinal ganglion cells. These factors may account for the discrepancy between authors (Claffei and Fiorentini, 1973, Ikeda and Wright, 1975, Kulikowski et al., 1979) with respect to the correlation between spatial and temporal receptive field properties.

Mustari et al. (1982) and Henry et al. (1983) found little correlation between the functional type of geniculate input to striate cortical cells and their time course of response to standing contrast.

Cell classification on the basis of the presence or absence of inhibitory sidebands has been used as the single or most important criterion for distinguishing between cortical cells (for example, Sherman et al., 1976; Dinse and von Seelen, 1981a,b). It divides the population of cortical cells in any one area rather reliably into two groups, and has the additional advantage of being independent of eccentricity. However, there is by no means a perfect correlation between cells with and without inhibitory sidebands and simple and complex cells respectively (for example, Albus and Fries, 1980). In addition, it is unnecessarily time-consuming to concentrate solely on areas of subliminal influence revealed only by subtle and often complex procedures (e.g. the injection of amino acids through multibarrelled electrodes to induce artificial discharge) at the expense of more readily observed differences in spatial organization of discharge regions.

A consideration of the classification scheme of Henry (1977) and Henry et al. (1978b), which attempts to deal with the acknowledged heterogeneity in the receptive field properties of complex cells as defined by Hubel and Wiesel (1962), highlights the problems involved in the use of functional criteria for cell classification. B-cells resemble complex cells in receptive field structure when tested with stationary flash-presented stimuli but, like simple cells, have sharply-peaking response profiles for moving stimuli, low spontaneous activity and narrow directional tuning. However, since these properties vary continuously from cell to cell, it is difficult in practice to use them as differentiating criteria. A more serious problem is that for some cells there is a complete lack of correlation between secondary response properties such as level of spontaneous activity and broadness of directional tuning (see section 7.2.). A further problem with classification schemes which incorporate functional criteria (Pettigrew et al., 1968; Henry, 1977; Henry et al., 1978b, 1979) is that they are difficult to apply in more than one cor-

tical area. Thus, the difference in velocity sensitivity of B- and C-cells found in area 17 (Henry, 1977; Henry et al., 1978b) does not obtain in area 18 (Orban et al., 1981a). Equally, however, the variation with eccentricity in properties within a single cortical area may make the strict application of functional criteria problematical. For example, if a simple cell had to fulfil the criterion of responding only to slow velocities (Pettigrew et al., 1968), this would all but exclude the possibility of encountering simple cells in area 18 or in regions of area 17 subserving peripheral vision.

5.1.2. The Present Classification Scheme

For each cell, quantitative data were available on a host of response properties, but, for the reasons outlined above, they were not used to *classify* cells. In the final analysis, C-, S-, B- and A-cells were classified on the basis of receptive field structure alone, as revealed by both stationary flash-presented and moving stimuli (see also Orban and Kennedy, 1981; Orban, 1984). The same classifying criteria and nomenclature were used for cells in both areas 17 and 18. Such a classification scheme has the virtue of allowing valid comparisons between different cells within a cortical area and between the same cells in different cortical areas with respect to functional properties, since these are not originally built into the classifying scheme.

The S-Cell

An S-cell was so classified if: (i) stationary bar stimuli of optimum orientation flashed at different locations across the receptive field, orthogonal to its axis orientation, disclosed a single ON or OFF zone, or a number of spatially offset, non-overlapping ON and OFF zones, and (ii) moving single light or dark edges swept across the receptive field (in a direction orthogonal to receptive field orientation) elicited a single, sharply-peaking response profile for one polarity of edge.

or a number of sharply-peaking, spatially offset response profiles for edges of either polarity. Note that cells for which both flash-presented and moving stimuli disclosed only one receptive field region were classified as S-cells, though they have almost certainly been classified in the past as complex (Hubel and Wiesel, 1962; Gilbert, 1977; Ferster, 1981). Further, since tests for spatial summation within subregions were not carried out, some of the remaining S-cells may also ultimately have been classified as complex by these authors.

The A-Cell

Cells which did not show the above correlation between receptive field structure as revealed by stationary flash-presented and moving stimuli were encountered infrequently, and classified as A-cells (Henry, 1977; Orban and Kennedy, 1981); they correspond to the non-uniform (Hubel and Wiesel, 1962) or discrete (Dean and Tolhurst, 1983) complex cells described previously. The absence of overlapping ON and OFF areas served to distinguish A-cells from complex cells, while their sustained response to moving stimuli extending over the entire discharge region precluded any allegiance with simple cells. The receptive fields of A-cells had either a single ON or OFF zone or a number of spatially separate ON and OFF subregions. At comparable eccentricities, A-cells invariably had wider minimum response fields than S-cells, and cells of both classes had minimum response field widths within the range reported by Orban and Kennedy (1981) and see Orban (1984) for S- and A-cells.

The C-Cell

If sensitive to stationary flash-presented stimuli, a C-cell exhibited a mixed ON/OFF response throughout the receptive field. Its discharge regions for moving edges of either polarity were overlapping, and it responded continuously throughout the traverse of a moving bar across the receptive field.

The B-Cell

Of the cells with overlapping ON and OFF zones in response to flash-presented stimuli, B-cells were distinguished from C-cells by their narrow, sharply-peaking response profiles for moving oriented stimuli. At comparable eccentricities, B-cells had narrower minimum response fields than C-cells, and cells of both classes had field widths within the range reported by Orban and Kennedy (1981, and see Orban, 1984) for B- and C-cells.

After the completion of this work, a quantitative study (Dean and Tolhurst, 1983) demonstrated a continuum between completely discrete and complete overlapping receptive field subregions in area 17 cells. The most frequent borderline cases in the present study were cells with spatially offset ON and OFF zones, but with a narrow intermediate strip of mixed ON/OFF discharge; these cells were classified as S-cells or A-cells according to their response profiles for moving stimuli.

Length Summation And End Inhibition

Quantitative length-response functions were derived for some 50% of cells in area 18 (see Chapter 7). In the remaining cells from both areas 17 and 18, assessments of the degree of length summation and end-inhibition were made using qualitative techniques. A distinction was made between cells with restricted and substantial length summation. However, cells were not rigidly subclassified as 'special' or 'standard' according to whether optimal bar length was significantly shorter than the height of the mapped receptive field (Gilbert, 1977), since the location of the lateral borders of the minimum response field is critically dependent on the length of the mapping stimulus used (see also Kato et al., 1978; Orban et al., 1979a,b). Cells in the present study with restricted length summation were comparable to the 'special complex' cells of Gilbert (1977), but did not include cells described by Hammond and Ahmed (1985) in which length summation is extensive, but less protracted than the height of the minimum response field.

Cells of each class were designated as end-inhibited (subscript $_H$) if an increase in bar length beyond the optimum produced an audible decrease in response magnitude. Using quantitative techniques and interleaved stimulus presentation Kato et al (1978) have found that contrary to earlier reports (Bodis-Wollner et al 1976 Gilbert, 1977, Rose, 1977a, Henry et al, 1978a), end-free and end-inhibited cells form two distinct populations. According to Kato et al (1978), the magnitude of end-inhibition detected qualitatively is close to the minimum value for end-inhibited cells identified by quantitative techniques.

Secondary Response Properties

The derivation of directional tuning curves for bar and noise motion (see below and Chapter 6) yielded quantitative data in all cells on level of spontaneous activity, width of directional tuning for bar motion and directional sensitivity. Directional tuning was defined by the vector of response magnitude for eighteen directions of motion, stepped in 10° intervals, through 360°. Width of directional tuning refers to the range of effective directions of bar motion. Directional sensitivity refers to the relative preference for one of two directions along a common axis. For direction-selective cells, bar motion in the non-preferred direction evoked a negligible response, no response at all, or suppression of spontaneous activity. Bidirectional cells had zero or weak bias for one of two directions along a common axis. Cells whose directional sensitivity fell between these two extremes were classified as direction-biased. Finally, qualitative assessments of ocular dominance (Hubel and Wiesel, 1962) were made in all cells. Important distinctions were made between cells which received comparable drive through either eye (ocular dominance groups 3-5) and those which were strongly monocularly-driven (ocular dominance groups 1, 2 and 6, 7).

Lamina-Of-Origin

Stereotaxic co-ordinates for penetrations in area 17 were chosen to avoid recording

exclusively from the superficial cortical layers down the medial bank of the lateral gyrus, to exclude the possibility of recording inadvertently from area 18, and to ensure that the electrode would sample during its traverse layers I-VI in sequence (see Methods). Thus, area 17 C-cells could be identified as residing in the deep or superficial layers with reference to the small-field, typically monocular simple cells of layer IV recorded in the same penetration, and tentatively on the basis of electrode depth (Hammond and MacKay, 1977; Hammond and Reck, 1980b; Hammond and Smith, 1982, 1983, 1984). In addition, it is now well established that strongly noise-sensitive complex cells of the striate cortex lie in two bands immediately above and below layer IV (Hammond and MacKay, 1977; Hammond, 1978c; Hammond and Reck, 1980b; Wagner et al., 1981; Hammond and Smith, 1982, 1983, 1984). The electrode rarely entered the white matter, but typically remained for many hundred μm in the deep layers during long penetrations down the medial bank.

For comparisons with area 17, it was desirable to subclassify area 18 C-cells according to lamina-of-origin. Compared with area 17, the most striking cytoarchitectonic feature of area 18 is that layer III is relatively wide, with its lower aspect situated about half way through the thickness of the cortex, and layer IV correspondingly narrow (Otsuka and Hassler, 1962; Garey, 1971; Harvey, 1980a; Humphrey et al., 1985a,b). Thus in area 18, the depth at which C-cells were encountered relative to S-cells in the same penetration provided a rather more reliable estimate of actual lamina-of-origin. In addition, little difficulty was experienced in distinguishing between superficial- and deep-layer C-cells on the basis of electrode depth; the choice of stereotaxic co-ordinates for penetrations in area 18 ensured that the electrode sampled during its traverse layers I-VI in sequence, and entered the white matter within 1,500-1,800μm of the cortical surface.

Responsiveness To Moving Visual Noise

All shades of noise sensitivity were encountered throughout the cortical lami-

nae. However, for comparisons between the noise sensitivity of different cell types within each cortical area and between cortical areas, cells were assigned to one of four groups on the basis of their responsiveness to moving noise.

Group IV cells were unresponsive to visual noise moving in any direction at any velocity.

Group III cells gave a weak response to moving noise which was related to the presence of non-uniformities of grain density in the noise sample; they responded specifically to certain (larger-than-average) black or white elements. Directional tuning for noise motion was ill-defined, and the selection of a fresh sample of noise either abolished the response or led to a predictable shift in the response peak as visualized in the dot display or in PSTHs. Group III cells were thus sensitive not to visual noise *per se*, but to the 'structure' within the noise sample.

The responses of *Group II* cells to moving noise were not related to the larger elements in the noise sample but did not exceed half the response to a moving contrast bar, with parameters optimized for each stimulus. Since in the same cell, both preferred direction and velocity tuning are typically different for noise and bar motion (Hammond, 1978c, 1981a,b; Hammond and Reck, 1980b; Hammond and Smith, 1983), assignment to a particular group on the basis of relative preference for noise and bar stimuli was made only after a comparison of directional tuning for the two stimuli over a range of velocities.

Group I cells responded vigorously to moving noise. They typically responded at least as well to noise as to bar motion and were frequently preferentially responsive to moving noise.

Thus, in what follows, cells in groups I and II are termed 'noise-sensitive', and those in groups III and IV 'noise-insensitive'. Among noise-insensitive cells, the 'structure-sensitive' cells of Group III are distinguished from Group IV cells, which were completely unresponsive to moving noise. Typical examples of the noise sensitivity of area 17 and area 18 C-cells in these groups are illustrated in Figs. 5.1

and 5.2.4). The distinction between Groups I and II was made because of the need for an objective measure of magnitude of response to moving noise and is admittedly rather arbitrary. However, the association described in sections 5.2 and 5.3 between group membership and secondary response properties may be considered to strengthen the validity of this distinction.

5.2. CELL CLASS AND NOISE SENSITIVITY: AREA 17

5.2.1. Synopsis

The noise sensitivity of different cell types in area 17 has been investigated extensively by others (Hammond and MacKay, 1975, 1977; Hammond, 1978c; Hoffmann et al., 1980; Hammond and Smith, 1982, 1983, 1984; Morrone et al., 1982). Preliminary recordings in area 17 were made merely to generate data for direct comparisons with results from area 18, using identical animal preparation, experimental procedure and cell classification. Quantitative data were obtained from 42 single cells in the striate cortex. These comprised 28 C-cells (2 C_{BI}), 5 B-cells, 8 S-cells (1 S_{BI}) and 1 A-cell, which were assigned to one of groups I-IV on the basis of their responsiveness to moving noise. The receptive field centres of all cells recorded in striate cortex lay in the lower contralateral quadrant of the visual field, within 10° of the area centralis projection. Receptive fields were divided into two eccentricity classes: 0-5° (19 cells); 5-10° (23 cells).

A break-down of area 17 cells according to cell class and responsiveness to moving noise is given in Table 5.1. C-cells dominated the sample in area 17, though because of sampling bias (see Discussion), the numbers of cells in each class are not representative of the relative proportions of each cell type in area 17. Eighty-two percent of C-cells were noise-sensitive, and the majority of noise-sensitive C-cells (78%) were assigned to Group I. A significant minority of C-cells (18%)

CELL CLASS	GROUP I	II	III	IV	
C	18 (64)	5 (18)	5 (18)	–	28 (2 C_M)
S	–	1 (13)	–	7 (88)	8 (1 S_M)
B	1 (20)	–	–	4 (80)	5
A	–	–	–	1 (100)	1
	19	6	5	12	42

LAMINA OF ORIGIN	GROUP I	II	III	IV	
SUPERFICIAL	3 (60)	–	2 (40)	–	5
DEEP	14 (70)	3 (15)	3 (15)	–	20 (2 C_M)
UNCERTAIN	1	2	–	–	3
	18	5	5	–	28

Table 5.1. Distribution of area 17 cells according to class (C, S, B, A) and noise sensitivity (membership of groups I–IV). Group I cells responded vigorously. Group II cells relatively weakly to moving noise. Group III cells were sensitive to the structure in the noise sample, and Group IV cells were completely unresponsive to moving noise (see text for details). Figures in parentheses indicate the percentage of cells within a given class in each group.

Table 5.2. Distribution of C-cells in area 17 according to lamina-of-origin (superficial layers or deep layers) and noise sensitivity (membership of groups I–IV). Figures in parentheses indicate the percentage of superficial-layer or deep-layer C-cells in each group.

was 'structure-sensitive', but no area 17 C-cell was completely unresponsive to moving noise. Noise-sensitive cells in the striate cortex were almost exclusively C-cells, one B-cell responded vigorously, one S-cell moderately well to moving noise.

5.2.2. C-Cells (67%)

(a) Superficial- And Deep-Layer C-Cells

Twenty-five of the 28 C-cells recorded in area 17 were identified as belonging to the superficial or deep layers. A break-down of area 17 C-cells according to lamina of origin and responsiveness to moving noise is given in Table 5.2. Most of the C-cells in the present sample were encountered in the deep layers. The majority of deep-layer C-cells (87%) were noise-sensitive, and most noise-sensitive deep-layer C-cells (82%) were assigned to Group 1. Indeed, strongly noise-sensitive, deep-layer C-cells comprised 50% of C-cells recorded in area 17. The small number of superficial-layer C-cells recorded either responded vigorously to moving noise or were 'structure-sensitive'.

(b) Receptive Field Width And Eccentricity

Of the 28 C-cells recorded in area 17, 13 (46%) had receptive field centres within 5° of the area centralis projection, and the field centres of the remaining 15 cells (54%) were in the eccentricity range 5–10°. Among Group 1 C-cells, 10 (56%) had receptive fields within and 8 (44%) beyond 5° of the area centralis projection. Group 1 C-cells comprised 77% of C-cells with receptive fields in the eccentricity class 0–5°, and 53% of C-cells with receptive fields more than 5° from the area centralis projection. There was no significant difference in receptive field width in these two eccentricity classes, either for the total population of C-cells (means 2·6°), or for deep-layer C-cells considered separately (means 2·5° and 2·7°). However, even when receptive fields in different eccentricity classes are pooled, the

numbers of C-cells outside Group I is too small to allow generalizations about the relative receptive field sizes of deep- and superficial-layer C-cells in different groups. Nevertheless, two features of receptive field width comparisons are worthy of mention. First, the receptive fields of the two noise-insensitive C-cells in the superficial layers were narrower (width at 1/8 eccentricity 7.10°) than those of all other C-cells. Second, among deep-layer C-cells, Group II cells had receptive fields which were narrower than the mean receptive field width of cells in Group I.

(c) Receptive Field Length

Major obvious differences in the receptive field dimensions of C-cells in different groups were observed along the longitudinal axis parallel to receptive field orientation. The length of C-cell minimum response fields was not correlated with membership of a particular group. However, 50% of Group I C-cells had receptive fields within which little length summation could be demonstrated, whereas all other C-cells showed substantial length summation.

(d) Secondary Response Properties

Group I C-cells had high spontaneous activity and broad directional tuning, showed strong directional bias and were typically direction-selective. With one exception, they received comparable drive through either eye or were only weakly dominated by one or other eye (ocular dominance groups 3–7, Hubel and Wiesel 1962). It is generally recognized however that, as a group, complex or C-cells in area 17 have relatively higher spontaneous activity (for example, Pettigrew et al. 1968; Gilbert 1977; Hammond and MacKay 1977; Henry 1977) and broader directional tuning (Henry et al. 1973; Watkins and Berkley 1974; Henry 1977; Hammond and Andrews 1978; Heggelund and Albus 1978; Leventhal and Hirsch 1978; Henry et al. 1979; Orban 1984) than simple or S-cells. Further, contrary to Hubel and Wiesel's (1962) initial finding that simple and complex cells do not differ in ocular dominance distribution, several authors (Albus 1975; Hammond and

MacKay, 1977; Gilbert, 1977; Leventhal and Hirsch, 1978; Orban and Kennedy, 1981; Berman et al., 1982) have reported that simple or S-cells are more often strongly dominated by one or other eye than complex or C-cells. Thus it is important to determine whether the properties of Group I C-cells simply reflect those of C-cells overall, or whether among C-cells there are differences in response properties which are associated with responsiveness to moving noise. The secondary response properties of C-cells in groups I, II and III are shown for comparison in Table 5.3. C-cells are not subdivided in the Table according to lamina of origin since only a small number of superficial-layer C-cells were recorded and their response properties were not obviously different from those of deep layer C-cells in the same group.

Spontaneous Activity

All C-cells recorded in the striate cortex were spontaneously active. Noise-sensitive C-cells had significantly higher spontaneous activity than noise insensitive C-cells (Mann Whitney U test, $P < 0.001$). However it is clear from Table 5.3 that this comparison masks a far more striking difference in level of spontaneous activity between C-cells in Group I and other C-cells. Among noise-sensitive C-cells those in Group I had appreciably higher spontaneous activity than those in Group II (Mann-Whitney U test, $P < 0.001$). Group II C-cells did not differ significantly in spontaneous activity from C-cells in Group III.

In the present sample, deep- and superficial-layer C-cells did not differ in spontaneous activity (means 17.8 and 17.2sp/s respectively). Among deep-layer C-cells those in Group I had considerably higher spontaneous activity (mean 23sp/s, range 10-52sp/s) than those in groups II and III (mean 6.6sp/s, range 0-17sp/s) (Mann Whitney U test, $P < 0.001$). In groups I and III, deep- and superficial layer C-cells had comparable spontaneous activity.

	SPONTANEOUS ACTIVITY (sp/s)	DIRECTIONAL TUNING WIDTH (deg.)	PERCENT DIRECTION SELECTIVE	PERCENT OCULAR DOMINANCE GROUPS 3 – 5
AREA 17				
GROUP I (n = 18)	24.5 (10 - 50, 11.4)	98.3 (60 - 180, 39.9)	67	72
GROUP II (n = 5)	7.0 (2 - 10, 3.2)	50.0 (30 - 80, 23.5)	20	—
GROUP III (n = 5)	5.0 (2 - 7, 2.7)	62.0 (30 - 80, 19.2)	—	40

Table 5.3. Properties of area 17 C-cells according to noise sensitivity (membership of groups I–III). Group I cells responded vigorously, Group II cells relatively weakly to moving noise. Group III cells were sensitive to the 'structure' in the noise sample (see text for details). Values for spontaneous activity and directional tuning width are means, with ranges and standard deviations in parentheses. Figures in the 3rd and 4th columns from the left indicate respectively, the percentage of C-cells in each group which were direction-selective, and which received good binocular drive (ocular dominance groups 3–5).

Directional Tuning Width

In Chapter 6, the directional tuning of area 17 C-cells for noise and bar motion is reported in detail, largely for comparison with the directional tuning of area 18 cells. Here, the directional tuning width, the total range of effective directions of bar motion of C-cells in different groups is compared. The two end-inhibited C-cells are included in these comparisons, since their directional tuning was not conspicuously broader than that of other C-cells within the same group.

There was no significant difference in the directional tuning width of noise-sensitive and noise-insensitive C-cells (means, 87° and 92°). However, among noise-sensitive C-cells, those in Group I were considerably more broadly tuned for direction than those in Group II (Mann-Whitney U test, $P < 0.01$). Group II C-cells did not differ significantly in directional tuning width from C-cells in Group III. It is worth emphasizing that no C-cell in either Group II or Group III had directional tuning as broad as the mean directional tuning width of Group I C-cells. The difference in directional tuning width between C-cells in Group I and other C-cells was highly statistically significant, both for C-cells overall and for comparisons of deep-layer C-cells alone (Mann-Whitney U test, $P < 0.01$). The directional tuning of superficial-layer C-cells was characteristic of that of C-cells in the groups to which they belonged: deep- and superficial-layer C-cells in Group I had comparable directional tuning, while in Group III the directional tuning of superficial-layer C-cells was relatively broad but not conspicuously broader than that of deep-layer C-cells.

It has been reported (Wilson and Sherman, 1976) that in striate cortex broadness of directional tuning is related directly with visual field eccentricity. However, the influence of receptive field eccentricity on broadness of directional tuning is negligible within 10° of the area centralis projection (Wilson and Sherman, 1976) where the receptive fields of all C-cells recorded in area 17 lay. In any event, a similar proportion of Group I C-cells had receptive fields in the eccentricity classes 0–5° and 5–10°, and Group I C-cells were predominant among C-cells with central

receptive fields. Group I C-cells with receptive fields within or beyond 5° of the area centralis projection had similarly broad directional tuning (mean widths 96.0° and 101.3°, which was broader than that of other C-cells with receptive fields in the same eccentricity class. Indeed, C-cells with receptive fields within 5° of the area centralis projection were more broadly tuned for direction than other C-cells, reflecting the predominance of Group I C-cells with receptive fields in this eccentricity class. Thus, at least for area 17 subserving central vision, broadness of directional tuning of C-cells would seem to be related to noise sensitivity rather than visual field eccentricity.

With their broad directional tuning and high spontaneous activity, strongly noise-sensitive Group I C-cells of the striate cortex are the archetypes of the C-cells of Henry (1977). However, a consideration of the response properties of C-cells in other groups highlights the problems inherent in the use of a classification scheme which incorporates both receptive field size and functional criteria. In some C-cells there was a distinct lack of correlation between level of spontaneous activity and broadness of directional tuning: the noise-insensitive superficial-layer C-cells had low spontaneous activity and rather broad directional tuning, while three C-cells in groups II and III had high spontaneous activity but were rather sharply tuned for direction (tuning width < 30°).

Directional Sensitivity

A high proportion of C-cells in Group I was direction-selective. C-cells in Group I were more often direction-selective than other C-cells (10%) (Fisher's exact probability test: $P < 0.01$). Seventy-one percent of deep-layer C-cells in Group I but none of the remaining deep layer C-cells were direction-selective. The difference in the proportion of direction-selective cells among C-cells in Group I and in Group II just failed to reach significance at the 5% level. Group III contained no direction-selective C-cells.

The proportion of direction-selective cells in area 17 is highest in regions subserving central vision and declines (gradually) with eccentricity (Orban et al., 1981b). However, the relatively high proportion of direction-selective Group I C-cells cannot be attributed to the relative predominance of Group I C-cells with receptive fields within 5° of the area centralis projection. First, the proportion of direction-selective cells among C-cells in Group I and among C-cells overall was similar for the two eccentricity classes 0–5° and 5–10°. Second, among C-cells with receptive fields within 5° of the area centralis projection, 60% of those in Group I, but none of those in groups II or III were direction-selective.

Ocular Dominance

A significantly higher proportion of C-cells in Group I received good binocular drive than did C-cells in other groups (Chi squared test, $P < 0.05$). The proportion of binocularly-driven C-cells in Group I might seem remarkably high considering the predominance of monocularly driven cells in striate cortex subserving central vision (0–4°) (Albus, 1975) and the relative predominance of Group I C-cells with receptive fields within 5° of the area centralis projection. However, the majority of complex cells with receptive fields in central and para-central projection areas are binocularly-driven (Albus, 1975). In addition, the sample of complex cells in the above study presumably contained some B-cells, which are known to be predominantly monocularly-driven (Orban, 1984). Thus for area 17 subserving central vision, the proportion of binocularly-driven cells may be even higher among C-cells than among complex cells. On the other hand, the proportion of complex cells with good binocular drive is lowest among cells with receptive fields in central projection areas (where Group I C-cells are in the majority) and increases with eccentricity (Albus, 1975). Thus it is noteworthy that, independent of receptive field eccentricity, the proportion of cells which received good binocular drive was higher among C-cells in Group I than among other C-cells.

All Group II C-cells and the superficial-layer C-cells of Group III were strongly

dominated by one or other eye. Two of the three deep-layer C-cells in Group III received strong binocular drive, but one of these was end-inhibited and might not be expected to respond to a stimulus of large areal extent such as moving noise.

However, the weak or absent response of C-cells to moving noise can not be attributed alone to the presence of **end-inhibition**. Group II C-cells were free of end-inhibition, while one Group I C-cell was end-stopped. On the other hand, 7/8 of Group I C-cells lacked the substantial length summation characteristic of C-cells in Groups II and III. Especially noteworthy, however, was one occasion on which three deep-layer direction-selective C-cells with high spontaneous activity and broad directional tuning were recorded consecutively in a single penetration. The first cell showed little length summation and no end-inhibition, the second both length summation and end-inhibition, and the third length summation but no end-inhibition. Despite obvious differences in requirements for stimulus length in these cells, they responded equally vigorously to moving noise.

The range of noise sensitivity of area 17 C-cells and its association with secondary response properties is illustrated in Fig. 7.1, which shows directional tuning for noise and bar motion of four C-cells (*A*–*D*) recorded during a single microelectrode penetration in area 17. Each pair of tuning curves is taken from a series of directional tuning comparisons made in the same cell over a range of velocities. The illustrated directional tuning curves were compiled using the velocity of motion which evoked the maximum response to moving noise.

The Group III superficial-layer C-cells *A* and *B* had relatively narrow receptive fields within which substantial length summation could be demonstrated. They were monocularly driven, had low spontaneous activity and were bidirectional for bar motion. Both were free of end-inhibition, but responded weakly to moving noise. The poor response to noise motion, due to excitation by the local configurations in the noise sample, gave rise to an ill-defined directional tuning curve with no clear peak. The first cell (*A*) was encountered close to the cortical surface and the second (*B*) rather deeper in the superficial layers, but probably still in the

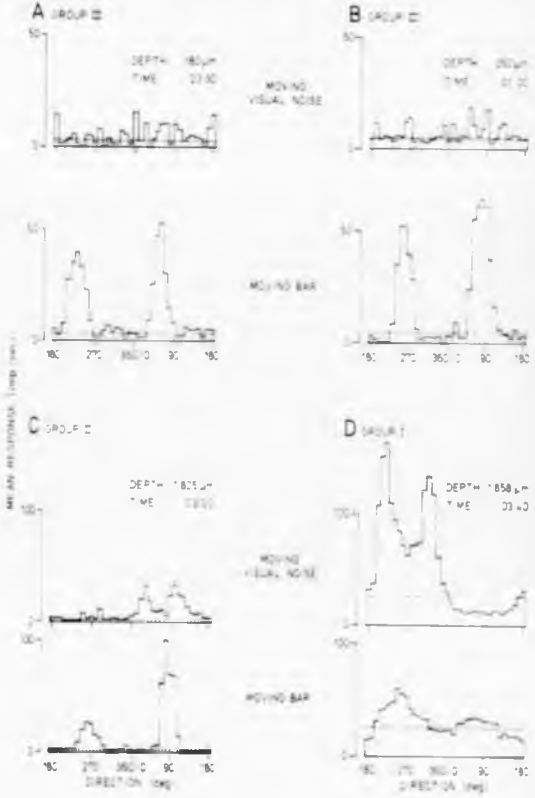

A
B
C
D
MOVING VISUAL NOISE
MOVING BAR
MEAN RF STRENGTH (imp sec⁻¹)
DIRECTION (deg)

Fig. 5.1. Directional tuning of 4 C-cells recorded in a single vertical penetration in area 17, for noise and bar motion interleaved, to illustrate the range in responsiveness to moving noise of area 17 C-cells. Direction stepped in 10° intervals, 4 responses per direction, spontaneous activity indicated by dotted lines. Each pair of directional tuning curves is taken from a series of directional tuning comparisons made over a range of velocities. Velocity of motion at which the illustrated tuning curves (*A*, *B*, *C*, *D*) were compiled was 8, 8, 12 and 12°/sec respectively. Note that in *C* and *D*, stimulus velocity is that which evoked the maximum response to moving noise. The depth and time at which each unit was encountered is indicated above each pair of tuning curves. The Group III C-cells encountered in the superficial layers (*A* and *B*) are sensitive not to moving noise *per se*, but to the structure within the noise sample, compared with the tuning profiles for bar motion; directional tuning for moving noise is relatively poorly defined with no clear peak. *C* and *D* show directional tuning comparisons for noise and bar motion in 2 noise-sensitive deep-layer C-cells. The Group I C-cell responds preferentially to the Group II C-cell relatively weakly to moving noise with velocity of motion optimal for that stimulus. Note the difference in magnitude of responsiveness to moving noise of 2 neighbouring deep-layer C-cells recorded within a period of 40 min, and its association with level of spontaneous activity and broadness of directional tuning. In *C* and *D*, directional tuning for noise motion is bimodal with depressed sensitivity in directions which are optimal for the moving bar. This underlines the importance of directional tuning comparisons in determining relative preference for noise or bar stimuli.

upper reaches of layer II/III. The remaining superficial-layer C-cells recorded were all strongly noise-sensitive, and were encountered deeper in the superficial layers presumably in layer III. Fig. 5.1C shows directional tuning for noise and bar motion of a deep-layer Group II C-cell recorded deep to two noise-insensitive S-cells. It was monocularly-driven, had low spontaneous activity and was direction biased for bar motion. Response to moving noise was relatively weak despite the absence of end-inhibition, but was not related to the structure in the noise sample. Directional tuning for moving noise was clearly bimodal with depressed sensitivity in directions which are most effective for bar motion (see Chapter 6). Fig. 5.1*D* illustrates an extreme example of a Group I C-cell recorded in the deep layers, which was preferentially responsive to moving noise. Although the response to bar motion was greater at lower velocities, compared with response to moving noise it was relatively weak throughout the effective velocity range (not illustrated). Note that the preferred directions for noise and bar motion were clearly different in this cell, and that comparisons of relative response magnitude were made for motion in the preferred direction for each stimulus. In the non-preferred direction, bar motion elicited a negligible response, while noise motion evoked strong suppression of firing (see Chapter 6). Compared with the C-cells representative of other groups, the Group I C-cell had relatively higher spontaneous activity and was more broadly tuned for direction of bar motion. The difference in magnitude of response to moving noise is remarkable in two deep-layer C-cells recorded in close proximity within a period of 40min (*C* and *D*).

5.2.3. B-Cells (12%)

Four of the 5 B-cells recorded in area 17 had receptive field centres located 5-10° from the area centralis projection. Mean receptive field width for these cells was 1.2°. The receptive field centre of the remaining B-cell (receptive field width 0.6°) lay within 5° of the area centralis projection. Three B-cells, which were all noise-insensitive, had the low spontaneous activity (mean 1sp/s) and narrow

directional tuning (mean tuning width 30°) characteristic of the B-cells of Henry (1977) and Henry et al. (1978b). The remaining B-cells showed a distinct lack of correlation between level of spontaneous activity and width of directional tuning: one B-cell in Group IV had the narrowest receptive field of all area 17 cells (0·6°) and zero spontaneous activity, but rather broad directional tuning (tuning width 40°), more typical of C-cells in Group I. The noise-sensitive B-cell, though not as broadly tuned for direction, had high spontaneous activity (8sp/s), among area 17 B-cells it had a relatively wide receptive field.

5.2.4. S-Cells (19%)

Of the 8 S-cells recorded in area 17, 6 had receptive fields within 5° of the area centralis projection. Mean S-cell receptive field width for the eccentricity classes 0–5° and 5–10° was 0·8° and 1·3°. Although all S-cells showed substantial length summation, none had the long, narrow receptive fields typical of layer VI simple cells (Gilbert, 1977). Area 17 S-cells had low or absent spontaneous activity (mean 1sp/s), narrow directional tuning (mean width 40·2°), were strongly dominated by one or other eye and, with one exception, were direction-selective. The end-inhibited S-cell had conspicuously broader directional tuning than fellow S-cells. Apart from its responsiveness to moving noise, the noise sensitive S-cell did not differ from other S-cells in secondary response properties, but had a relatively wide receptive field.

5.2.5. A-Cells (2%)

The single A-cell recorded in area 17 was unresponsive to moving noise. It had higher spontaneous activity (6sp/s) and broader directional tuning (tuning width 75°) than any area 17 S-cell, and received comparable drive through either eye.

5.3. CELL CLASS AND NOISE SENSITIVITY: AREA 18

5.3.1. Synopsis

Quantitative data were obtained from 67 single cells in area 18. These comprised 37 C-cells (7 C_B), 10 B-cells, 16 S-cells (3 S_B), and 4 A-cells (1 A_B) whose receptive fields lay within 18° of the area centralis projection. Electrode placement within conservative H-C coordinates (see section 4.4.2.) left relatively unexplored the medial part of area 18 flanking the projection of the vertical meridian, and only 11 area 18 cells (17%) had receptive fields within 5° of the area centralis projection. The receptive fields of 37 cells (55%) were in the eccentricity range 5–10°, and 19 cells (28%) had receptive fields more than 10° from the area centralis projection.

A break-down of area 18 cells according to class and responsiveness to moving noise is given in Table 5.4. Because of sampling bias (see Discussion), the numbers of C-, B-, S-, and A-cells are not representative of the relative proportions of each cell type in area 18. C-cells were the most frequently encountered cell type (55%), though in area 18 they formed a slightly lower proportion of recorded cells than in area 17. The majority of C-cells in area 18 (65%), like their counterparts in area 17, were noise-sensitive; they are found predominantly in Group I. The difference in the proportions of noise-sensitive C-cells in area 17 (82%) and area 18 was not statistically significant, nor was there any significant difference in the proportions of area 17 and area 18 C-cells assigned to Group I (64% and 54% respectively). However, whereas no C-cell in area 17 was unresponsive to moving noise, a significant minority (14%) of C-cells in area 18 belonged to Group IV; they comprised 39% of noise-insensitive C-cells in this area. As in area 17, C-cells dominated Group I, though in area 18 one S-cell was found in this group. A similarly low proportion of S-cells in area 17 (13%) and area 18 (12%) was noise-sensitive. Compared with their counterparts in area 17, a relatively higher proportion of B-cells in area 18 was responsive to moving noise. However, the

CELL CLASS	GROUP I	II	III	IV	
C	20 (54)	4 (11)	8 (22)	5 (14)	37 (5 C_M)
S	1 (6)	1 (6)	2 (13)	12 (75)	16 (3 S_M)
B	1 (10)	3 (30)	1 (10)	5 (50)	10
A	–	–	–	4 (100)	4
	22	8	11	26	67

LAMINA OF ORIGIN	GROUP I	II	III	IV	
SUPERFICIAL	5 (33)	4 (27)	5 (33)	1 (7)	15 (1 C_M)
DEEP	15 (75)	–	3 (15)	2 (10)	20 (3 C_M)
UNCERTAIN	–	–	–	2	2 (1 C_M)
	20	4	8	5	37

Table 5.4. Properties of area 18 cells according to class (C, S, B, A) and noise sensitivity (membership of groups I–IV). Group I cells responded vigorously. Group II cells relatively weakly to moving noise. Group III cells were sensitive to the structure in the noise samples, and Group IV cells were completely unresponsive to moving noise (see text for details). Figures in parentheses indicate the percentage of cells within a given class in each group.

Table 5.5. Distribution of C cells in area 18 according to lamina-of-origin (superficial layers or deep layers) and noise sensitivity (membership of groups I–IV). Figures in parentheses indicate the percentage of superficial-layer or deep-layer C cells in each group.

sample of B-cells from the two cortical areas was small and this difference did not reach statistical significance. A-cells in both areas 17 and 18 were unresponsive to moving noise.

5.3.2. C-Cells (55%)

(a) Superficial- And Deep-Layer C-Cells

All but two C-cells recorded in area 18 could be identified as belonging to the superficial or deep layers. A break-down of area 18 C-cells according to lamina-of-origin and responsiveness to moving noise is given in Table 5.5. Compared with area 17, a relatively higher proportion of C-cells in area 18 (40%) were encountered in the superficial layers. However, as in area 17, deep-layer C-cells were in the majority (54%) and, compared with superficial-layer C-cells, they formed a relatively higher proportion (62%) of noise-sensitive C-cells recorded in area 18.

There was no significant difference in the proportion of noise-sensitive C-cells in the deep- and superficial layers (75% and 60% respectively), though a relatively higher proportion of deep layer C-cells were in Group I (Chi squared test, $P < 0.05$). Further, among noise-sensitive C-cells, deep-layer C-cells were confined to Group I, whereas superficial-layer C-cells were distributed rather evenly between groups I (53%) and II (47%).

A similar proportion of deep-layer C-cells in areas 17 (70%) and 18 (75%) were Group I cells, and the difference in the proportion of deep-layer C-cells in the two cortical areas which were noise-sensitive (area 17, 85% and area 18, 77%) was not statistically significant. Indeed, the responsiveness to bar motion of one apparently noise-insensitive C-cell in area 18 was highly variable and inversely correlated with level of spontaneous activity. If this cell is excluded from the sample on the assumption that it was damaged and may ultimately have responded

to moving noise, the proportion of noise-sensitive C-cells in area 18 reaches 79%. An identical proportion (60%) of superficial-layer C-cells in areas 17 and 18 was noise-sensitive, though the small sample of superficial-layer C-cells in area 17 restricts the validity of this comparison. The lower proportion of noise-sensitive C-cells in area 18 compared with area 17 (sections 5.2.1 and 5.3.1.1, though statistically insignificant, could be attributed almost entirely to the relatively higher proportion of superficial-layer cells among the sample of area 18 C-cells. It remains to be determined whether an increase in sample size would reveal a significant difference in the noise sensitivity of deep- and superficial-layer C-cells in area 18.

(b) Receptive Field Width And Eccentricity

Whereas in area 17, widths of C-cell receptive fields in the eccentricity classes 0–5° and 5–10° were not significantly different, the receptive field width of C-cells in area 18 increased with eccentricity. This is consistent with Orban and Kennedy's (1981) finding that the receptive field width of C-cells increases far more steeply with eccentricity in area 18 than in area 17. Mean receptive field width for the eccentricity classes 0–5° (6 cells), 5–10° (21 cells), and 10–18° (8 cells) was 3·1°, 4·1°, and 5·9°, respectively. The vast majority (80%) of Group I C-cells had receptive fields in the eccentricity range 5–10°. Ten percent had receptive fields within 5° or beyond 10° of the area centralis projection. Group I C-cells comprised 33%, 70% and 27% of C-cells with receptive fields in the eccentricity classes 0–5°, 5–10° and 10–18°, respectively.

Since in area 18 relatively few C-cells were encountered with receptive field centres within 5° or beyond 10° of the area centralis projection, receptive field width comparisons could be made only among cells with receptive fields in the eccentricity class 5–10°. Within this range, there was no significant difference in receptive field width of deep- and superficial-layer C-cells (mean widths 4·2° and 4·1°, respectively). Deep-layer C-cells outside Group I with receptive fields in the eccentricity

class 5–10° were too few in number to allow valid comparisons of receptive field width between deep-layer C-cells in different groups. Among superficial layer C-cells, those in Group I had significantly wider receptive fields (mean width 5·1°) than those in other groups (mean width 3·0°) (Mann Whitney U test, $P = 0{\cdot}029$), thus paralleling the difference in receptive field width between noise-sensitive and noise-insensitive superficial-layer C-cells in area 17. The difference in receptive field width of superficial- and deep-layer C-cells (mean width 4·1°) in Group I did not reach statistical significance. Among Group I C-cells, those in the superficial layers had homogeneously wide receptive fields (range 4·2–6·6°), whereas those in the deep layers had more widely ranging receptive field widths (2·0–6·8°), though this difference may simply reflect a difference in the number of deep- and superficial-layer C-cells in Group I.

(c) Receptive Field Length

As in area 17, a relatively high proportion of Group I C-cells in area 18 (50%) had receptive fields within which little length summation could be demonstrated, whereas only 24% of C-cells outside Group I showed this type of summatory behaviour. Since one of the characteristics of end-inhibited cells is their restricted length summation (Kato et al. 1978), and since end-inhibited cells might be expected *a priori* to respond weakly to moving noise, it is important to determine whether their inclusion in the above comparisons blurs an otherwise absolute correlation between type of summatory behaviour and responsiveness to moving noise. In fact, the removal of end-inhibited cells leads to a decline in the proportion of cells with restricted length summation both among C-cells in Group I (44%) and among other C-cells (14%). On the other hand, 71% of all C-cells with restricted length summation, and 80% of end-free C-cells showing this type of summatory behaviour were Group I C-cells. Thus, as in area 17, most C-cells in area 18 which lacked substantial length summation are in Group I, though localized length summation is not a necessary condition for good noise sensitivity. Conversely, the

existence of end-inhibition does not preclude vigorous responsiveness to moving noise.

(d) Secondary Response Properties

The most interesting aspect of the present results was the striking similarity in response properties of Group I C-cells in area 17 and area 18 (see Table 5.6). Indeed, Group I C-cells in the two cortical areas were more alike in response properties than cells of different classes in the same cortical area. Like their counterparts in area 17, Group I C-cells in area 18 had high spontaneous activity, were broadly tuned for direction, almost invariably direction-selective, and with few exceptions received comparable drive through either eye. These generalizations apply equally to deep and superficial-layer Group I C-cells, though those in the deep layers were more homogeneous in spontaneous activity and ocular dominance.

Because of the known association between receptive field structure and secondary response properties of cells in area 18, it is important to determine whether, as in area 17, the properties of Group I C-cells in area 18 are distinctive, or whether they are characteristic of those of C-cells overall. It has been reported that in area 18, C-cells have higher spontaneous activity and broader directional tuning than S- or B-cells (Harvey, 1980a,b; Orban, 1984), although Hammond and Andrews (1978) found no substantial difference in tuning width of complex type 1 and type 2 cells (equated respectively with area 17 simple and complex cells). Compared with area 17, area 18 contains a relatively higher proportion of monocularly driven cells (Orban and Kennedy, 1981), though, according to Ferster (1981), this difference applies only to the superficial layers of the two cortical areas. Nevertheless, in area 18, C-cells more often receive strong binocular drive than do S-cells (Harvey, 1980a,b; Orban, 1984). Finally, area 18 contains a higher proportion of direction-selective cells than does area 17 (Ferster, 1981; Orban et al., 1981b), though pronounced direction selectivity seems to be associated with S-cells (Orban et al., 1981b). Table 5.6 shows the properties of area 18 C-cells in Group I together

	SPONTANEOUS ACTIVITY (sp/s)	DIRECTIONAL TUNING WIDTH (deg.)	PERCENT DIRECTION SELECTIVE	PERCENT OCULAR DOMINANCE GROUPS 3–5
AREA 17				
GROUP I (n = 18)	24.5 (10 - 50; 11.4)	98.3 (40 - 180; 39.9)	67	72
AREA 18				
GROUP I (n = 20)	10.0 (0 - 25; 6.0)	109.4 (40 - 180; 46.4)	85	75
GROUP I (n = 15) (deep layer)	11.7 (5 - 25; 4.9)	109.2 (40 - 180; 45.1)	93	87
GROUP II (n = 4)	4.3 (0 - 9; 4.0)	100.0 (60 - 180; 75.5)	50	75
GROUP III (n = 8)	2.8 (0 - 9; 3.9)	78.5 (40 - 130; 38.2)	25	13
GROUP IV (n = 5)	5.6 (0 - 10; 5.5)	66.3 (60 - 80; 9.5)	—	—

Table 5.6. Properties of area 18 C-cells according to noise sensitivity (membership of groups I–IV), and those of area 17 Group I C-cells for comparison. The properties of deep-layer C-cells in Group I are shown separately. Group I cells responded vigorously, Group II cells relatively weakly to moving noise. Group III cells were sensitive to the 'structure' within the noise sample and Group IV cells were unresponsive to moving noise (see text for details). Values for spontaneous activity and directional tuning width are means, with ranges and standard deviations in parentheses. Note that C_B-cells are excluded from comparisons of directional tuning width. Figures in the 3rd and 4th columns from the left indicate respectively the percentage of C-cells in each group which were direction selective and which received good binocular drive (ocular dominance groups 3–5)

with those of C-cells in other groups for comparison.

Spontaneous Activity

Noise-sensitive C-cells had significantly higher spontaneous activity (mean 2·6sp/s) than noise-insensitive C-cells (mean 1·1sp/s) (Mann-Whitney U test $P = 0.01$). However, as in area 17, the striking differences in spontaneous activity were between Group I C-cells and C-cells in other groups. Among noise-sensitive C-cells, those in Group I had higher spontaneous activity than those in Group II (Mann-Whitney U test $P < 0.05$). Group I C-cells had considerably higher spontaneous activity than noise-insensitive C-cells (Mann-Whitney U test, $P < 0.02$), while there was no difference in spontaneous activity between noise-insensitive C-cells and C-cells in Group II. Among noise-insensitive C-cells, members of groups III and IV did not differ significantly in spontaneous activity, but deep-layer C-cells had significantly higher spontaneous activity (mean 0·9sp/s) than superficial-layer C-cells (mean 0·5sp/s) (Mann Whitney U test $P < 0.01$). Similarly, among Group I C-cells, those in the deep layers had significantly higher spontaneous activity than those in the superficial layers (mean 5·2sp/s) (Mann-Whitney U test $P < 0.05$), though superficial-layer C-cells in Group I formed a rather heterogeneous group with respect to spontaneous activity (range 0·10sp/s). Overall, deep-layer C-cells had significantly higher spontaneous activity (mean 10·4sp/s) than superficial-layer C-cells (mean 3·1sp/s). However, the relatively high spontaneous activity of Group I C-cells is not due solely to the fact that deep-layer C-cells form the majority of C-cells in Group I, but are in the minority among other C-cells. The higher spontaneous activity of Group I C-cells compared with noise-insensitive C-cells reaches statistical significance when either deep-layer or superficial-layer C-cells are considered separately (Mann-Whitney U test $P < 0.05$ and $P < 0.01$ respectively).

Although Group I C-cells in both cortical areas had relatively high spontaneous activity, those in area 17 had significantly higher spontaneous activity than those in

area 18 (Mann-Whitney U test, $P < 0.001$). The difference in spontaneous activity of Group I C-cells in the two cortical areas is also significant when only deep-layer cells are compared (Mann-Whitney U test $P < 0.01$). These differences reflect the lower spontaneous activity of area 18 C-cells overall (mean 7·8sp/s) compared with their area 17 counterparts (mean 16·4sp/s) (Mann-Whitney U test $P < 0.005$).

Directional Tuning Width

The directional tuning of area 18 cells for noise and bar motion is reported in detail in Chapter 6. Present results are restricted to comparisons among C-cells of width of directional tuning for bar motion.

The small number of area 18 C-cells recorded with receptive fields within 5° or beyond 10° of the area centralis projection precluded a detailed analysis of the influence of receptive field eccentricity on broadness of directional tuning. However, there was no indication in the present data that directional tuning width of C-cells increased with receptive field eccentricity. Moreover, Orban and Kennedy (1981) found no significant correlation between receptive field eccentricity and *qualitatively* determined directional tuning width of area 18 cells with receptive fields distributed over a much wider range of eccentricities. Thus, for comparisons of directional tuning width of C-cells in different groups, cells with receptive fields in different eccentricity classes were pooled. Since two C_B-cells had conspicuously broader directional tuning than fellow C-cells in the same group, all C_B-cells were excluded from the present directional tuning comparisons.

Noise-sensitive C-cells were significantly more broadly tuned for direction (mean width 108·1°) than noise-insensitive C-cells (mean width 74·1°) (Mann-Whitney U test, $P < 0.05$). There was no significant difference in directional tuning width between the noise-sensitive C-cells of groups I and II, or between the noise-insensitive C-cells of groups III and IV. This is in contrast to the situation in area 17 where Group I C-cells had considerably broader tuning than Group II C-

cells, and the difference in directional tuning of noise-sensitive and noise-insensitive C-cells did not reach statistical significance. However, the number of end-free C-cells in Group II is too small to conclude that this represents an areal difference or is due to the fact that Group II C-cells in area 17 were all recorded in the deep layers, whereas area 18 Group II C-cells were exclusively superficial-layer cells. The directional tuning width of Group II C-cells has a conspicuously high standard deviation: one Group II C-cell had a directional tuning width (180°) three times as broad as that of other C-cells in this group. On the other hand, the C-cell in this group which was excluded from the present comparisons had broad directional tuning (width 120°). What is clear however is that, as in area 17, Group I C-cells were appreciably more broadly tuned for direction than noise-insensitive C-cells. This difference is more highly statistically significant (Mann-Whitney U test: $P < 0.025$) than that between noise-sensitive and noise-insensitive C-cells overall.

Among Group I C-cells, those in the deep and superficial layers had almost identical directional tuning (mean widths: 109.2° and 110.0°, respectively), thus reflecting the overall similarity in directional tuning of deep- and superficial-layer C-cells (overall mean width: 99.7° and 93.4°). However, deep- and superficial-layer C-cells in different groups differed markedly in directional tuning: deep- and superficial-layer C-cells in Group I were appreciably more broadly tuned for direction than their noise-insensitive counterparts (mean widths: 63.9°, 76.7°) (Mann-Whitney U test: $P < 0.05$).

Thus, noise sensitivity would seem to be a better predictor than receptive field eccentricity or lamina of origin of the directional tuning width of C-cells in areas 17 and 18. Group I C-cells in areas 17 and 18 had comparable directional tuning widths, thus reflecting the overall similarity in directional tuning of C-cells in the two cortical areas (mean widths: area 17, 83.2°; area 18, 96.4°).

Direction Sensitivity

Noise-sensitive C-cells were more often direction-selective (79%) than noise-insensitive C-cells (18%) (Chi-squared test, $P < 0.001$). This difference is due almost entirely to the high proportion of direction-selective cells among C-cells in Group I; there is no difference in the proportion of direction-selective cells among Group II C-cells and noise-insensitive C-cells, while a significantly higher proportion of C-cells in Group I compared with other C-cells was direction-selective (Chi-squared test, $P < 0.001$). Eighty-one percent of direction-selective C-cells recorded in area 18 were in Group I.

There was no significant difference in the proportion of direction-selective cells among deep-layer and superficial-layer C-cells (70% and 40% respectively). The proportion of direction-selective superficial-layer C-cells was highest in Group I (60%), but not significantly higher than that in other groups. Direction-selective deep layer C-cells, on the other hand, were confined to Group I. All but one deep-layer C-cell in Group I was direction-selective, and Group I deep layer C-cells in turn constituted 67% of all direction-selective C-cells in area 18. Direction-selective Group I C-cells in the superficial layers, and most of those in the deep layers showed suppression of firing for bar motion in the non-preferred direction, at least at some velocities (see Chapter 6).

Orban et al. (1981b) have reported that the proportion of direction-selective cells in area 18 is highest in regions subserving central vision (0-5°) and declines relatively steeply with eccentricity within 10° of the area centralis projection. The relatively high proportion of direction-selective cells among C-cells in Group I is thus all the more remarkable since only 10% of Group I C-cells had receptive fields within 5° of the area centralis projection, and Group I C-cells comprised only 33% of all C-cells with receptive fields in this eccentricity class. Among C-cells with receptive fields in the eccentricity class 0-5°, all Group I C-cells, but only 25% of other C-cells were direction-selective. The proportion of direction-selective C-cells was highest among C-cells with receptive fields within 5-10° of the area centralis

projection corresponding with the relative and absolute predominance of Group I C-cells with receptive fields in this eccentricity range. However, independent of eccentricity, Group I C-cells were more likely to be direction-selective than other C-cells.

There was no significant difference in the proportion of direction-selective cells among Group I C-cells in area 17 (67%) and area 18 (62%), reflecting the overall similarity in the proportion of direction-selective C-cells recorded in the two cortical areas (area 17: 46%; area 18: 57%). This result is not, however, inconsistent with reports that area 18 contains a higher proportion of direction-selective cells than area 17 (Forster, 1981; Orban et al., 1981b). In the present study, a relatively lower proportion of area 18 C-cells, compared with those in area 17, had receptive fields within 5° of the area centralis projection, where the difference in the proportions of direction-selective cells in the two cortical areas is known to be most pronounced (Orban et al., 1981b). Thus, comparisons of areas 17 and 18 subserving central vision may have yielded a significant difference in the proportion of direction-selective cells among C-cells in the two cortical areas. In this context, it is noteworthy that the difference in the proportion of direction-selective cells among deep-layer C-cells in areas 17 and 18 almost reached statistical significance at the 5% level.

Ocular Dominance

Like their counterparts in area 17, Group I C-cells in area 18 typically received comparable drive through either eye. Table 5.6 shows that this association is stronger when deep-layer Group I C-cells are considered separately: noise-sensitive superficial-layer C-cells were equally likely to receive either predominantly monocular or good binocular drive, and only 40% of superficial-layer C-cells in Group I received comparable drive through either eye. With one exception (an end-inhibited deep-layer C-cell), C-cells in groups III and IV were strongly dominated by one or other eye. The majority of monocularly-driven cells (78%) were dominated by

the contralateral eye.

Since in area 18, cells with receptive fields within 10° of the area centralis projection are more often monocularly-driven than those with more peripheral receptive fields (Orban, 1984), it is important to establish that the observed difference in ocular dominance distribution of C-cells in different groups does not stem simply from pooling cells with receptive fields in different eccentricity classes. Most C-cells (78%) and the vast majority of those in Group I (90%) had receptive fields within the eccentricity range 0–10°. In addition, Group I C-cells with more peripheral receptive fields (10–18°) all received good binocular drive, whereas 66% of the remaining C-cells with receptive fields in this eccentricity class were strongly dominated by one or other eye. In view of the finding that, at least in area 17, the proportion of monocularly-driven cells is highest in regions subserving central vision (0–4°) and declines steeply with eccentricity (Allen, 1975), it should be emphasized that in area 18, a mere 10% of Group I C-cells had receptive fields within 5° of the area centralis projection and that Group I C-cells comprised only 33% of C-cells with receptive fields in this eccentricity class. On the other hand, among C-cells with receptive fields within 5° of the area centralis projection, Group I C-cells received strong binocular drive, whereas all other C-cells were strongly dominated by one or other eye. Indeed, independent of receptive field eccentricity, C-cells in Group I received comparable drive through either eye more often than other C-cells.

The range of noise sensitivity of C-cells in area 18 and its association with secondary response properties is illustrated in Fig. 5.2, which shows directional tuning comparisons for noise and bar motion in four C-cells (*A*–*D*), each representative of one of groups I–IV. Each pair of directional tuning curves is taken from a series of directional tuning comparisons made in the same cell over a range of velocities. The illustrated directional tuning curves in *A* and *B* were compiled using the velocity of motion which evoked the maximum response to moving noise

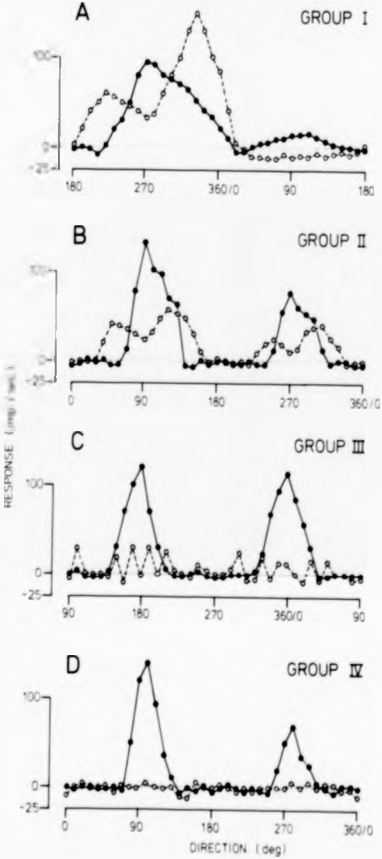

A
GROUP I
100
0
-25
180
270
360/0
90
180
B
GROUP II
100
0
-25
0
90
180
270
360/0
C
GROUP III
100
0
-25
90
180
270
360/0
90
D
GROUP IV
100
0
-25
0
90
180
270
360/0
RESPONSE (imp / sec)
DIRECTION (deg)

Fig. 5.2. Directional tuning of 4 area 18 C-cells (*A*, *B*, *C*, *D*), representative of groups I, II, III and IV, for bar and noise motion interleaved (solid and broken lines respectively). Direction was stepped in 10° intervals. Response magnitude was derived from PSTHs (4 responses per direction) and expressed as peak firing frequency (averaged over 3 adjacent bins centred on the bin containing the highest spike count), subtracted from mean spontaneous activity assessed at the time each PSTH was compiled. Information about absolute levels of spontaneous activity is thus lost in these plots. Each pair of directional tuning curves is taken from a series of directional tuning comparisons, derived over a range of velocities. The illustrated directional tuning curves in *A* and *B* were compiled using stimulus velocity which evoked the maximum response to moving noise (30 and 75°/sec respectively). Note the range of noise sensitivity of area 18 C-cells and its association with width of directional tuning and directional sensitivity.

Because of the wide range of effective velocities of cells in area 18, response is expressed not as the mean number of impulses/sweep, but as peak firing frequency (see Methods).

The two C-cells in *A* and *B* were noise-sensitive. The Group I C-cell (*A*) responded preferentially, the Group II C-cell (*B*) relatively weakly to visual noise moving at the optimal velocity for that stimulus. Though the relative preference of the Group I C-cell for noise and bar motion altered with velocity, the maximum response to each stimulus was of comparable magnitude (not illustrated). The C-cell in *A* was typical of Group I C-cells in its broad directional tuning for bar motion and direction selectivity. In the non-preferred direction, bar motion evoked a negligible response, while noise motion suppressed spontaneous firing. In contrast, the Group II C-cell (*B*) was relatively sharply tuned for direction, and showed only weak bias for one of two directions of motion along the preferred axis. In contrast to the Group I C-cells which had high spontaneous activity (>sp/s) and restricted length summation, the Group II C-cell had relatively low spontaneous activity (2sp/s) and summation for stimulus length well beyond the borders of the minimum response field.

Compared with the Group I C-cell, the noise-insensitive C-cells in *C* and *D* were both relatively narrowly tuned for direction. They lacked spontaneous activity, were monocularly-driven and showed substantial length summation. The Group III C-cell was sensitive to the 'structure' in the noise sample and directional tuning for moving noise was ill-defined. The Group IV C-cell was neither excited nor inhibited by moving noise.

5.3.3. B-Cells (15%)

Ten B-cells were recorded in area 18. Four B-cells had receptive field centres between 5–10° of the area centralis projection, and the receptive fields of the remaining 6 B-cells were in the range 10–18°. Mean B-cell receptive field width for

these eccentricity classes was 1·5° and 2·4°. The receptive fields of noise-sensitive B-cells lay more than 10° from the area centralis projection, and all were wider than those of noise-insensitive B-cells with receptive fields in the same eccentricity class. Of the four noise-sensitive B-cells in area 18, three responded weakly and one responded vigorously to moving noise. The difference in the proportion of noise-sensitive B-cells in area 17 (20%) and area 18 (40%) was not statistically significant. With one exception, area 18 B-cells were recorded in the superficial layers. As a group they had narrow directional tuning (mean width 68·0°, range 20–100°), low spontaneous activity (mean 2·5sp/s, range 0–16sp/s) and tended to be dominated by one or other eye. However, whereas B-cells in groups III and IV were silent in the absence of visual stimulation, noise-sensitive B-cells were all spontaneously active (mean 6·3sp/s), and the B-cell in Group I had a high resting discharge (10sp/s).

5.3.4. S-Cells (24%)

Of the 10 S-cells recorded in area 18, 3 had receptive field centres within 5° of the area centralis projection. Eight S-cells had receptive fields in the eccentricity range 5–10°, and the receptive fields of the remaining 5 cells lay between 10–18° of the area centralis projection. Mean receptive field widths for each eccentricity class were 1·2°, 2·0° and 2·8°. Like their counterparts in area 17, S-cells in area 18 had zero or low resting discharge, showed substantial length summation, were strongly dominated by one or other eye, and were predominantly direction-selective for bar motion. With the exception of end-inhibited members, S-cells were narrowly tuned for direction of motion (mean width 57·3°, range 40–90°). Among area 18 S-cells those responsive to moving noise were unique in being spontaneously active. Their receptive fields lay more than 10° from the area centralis projection.

S-cells having only one receptive field subregion, which would have been classified as complex by Hubel and Wiesel (1962), resembled other S-cells in receptive field properties and were unresponsive to moving noise.

5.3.5. A-Cells (6/7)

Four A-cells were recorded in area 18, one of which had only a single receptive field subregion. Two A-cells had receptive field centres within 5° of the area centralis projection, and the field centres of the remaining A-cells were in the range 5–10°. Area 18 A-cells had rather low spontaneous activity (mean 2sp/s), broad directional tuning (mean width 75·0°) and, in common with the A-cell recorded in area 17, were unresponsive to moving noise.

5.4. VARIABILITY IN RESPONSIVENESS TO NOISE AND BAR MOTION

Some aspects of the variability in responsiveness to moving noise are worthy of mention. The high short-term response variability in the lightly anæsthetized visual cortex might be expected to influence responses to bar and noise stimuli to a similar extent. Interestingly, however, there were a number of cases of *differential* variability in the responsiveness of the same cell to noise and bar motion. A minority of cells preliminarily classified as weakly noise-sensitive later showed preferential responsiveness to moving noise as evinced by directional tuning comparisons for noise and bar motion. In addition, it was possible on occasions to selectively improve responsiveness to moving noise by lightening anæsthesia as far as was consistent with satisfactory monitoring criteria of behavioural state. Exceptionally, short-term differential response variability was observed during the time taken to compile a single pair of directional tuning curves. Three examples of such differential variability are illustrated in Fig. 5.3.

Figs. 5.3*A*, *B* and *C* depict, in the form of dot raster displays, the on-line registration of neural impulses, for three single cells in area 18. The duration of each sequence, which represents responses to forward and reverse sweeps of visual noise and bar stimuli along a common axis for eighteen axes of motion, plus

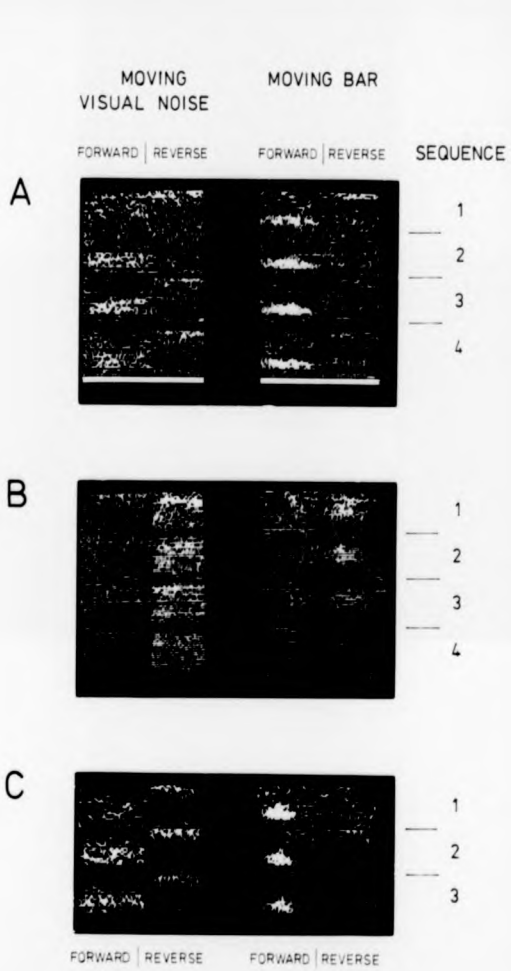

MOVING VISUAL NOISE
MOVING BAR
FORWARD | REVERSE
FORWARD | REVERSE
SEQUENCE
A
1
2
3
4
B
1
2
3
4
C
1
2
3
FORWARD | REVERSE
FORWARD | REVERSE

Fig. 5.3. Photographs of dot raster displays illustrating extreme examples of short-term differential variability in response to noise and bar motion, during the compilation of a single pair of directional tuning curves, in each of 3 area 18 cells (*A*, *B*, *C*). Each dot represents a single cell spike. Each sequence represents responses to forward and reverse sweeps of visual noise and bar stimuli along a common axis for 18 axes of motion followed by 3 cycles of spontaneous activity. The duration of each sequence is approximately two-and-a-half min. The 3 examples illustrate selective short-term variability in response to moving noise (*A*), a relatively steeper decline with time in responsiveness to bar motion (*B*), and in *C*, an increase in responsiveness to noise motion and a simultaneous decrease in responsiveness to bar motion. The continuous horizontal lines in *A* represent calibration pulses. In *C*, compilation of the directional tuning curve was interrupted after the 3rd sequence.

three cycles of resting discharge, is approximately two-and-a-half minutes. In Fig. 5.3*A* responsiveness to moving noise increases dramatically from sequence one to two, remains constant from sequence two to three, and declines steeply during the fourth sequence. In contrast, the response to the moving bar remains relatively constant throughout the compilation of the directional tuning curve, though there is some indication of a slight improvement in responsiveness with time. In Fig. 5.3*B*, responsiveness to moving noise remains rather constant after an initial decline from sequence one to two, whereas responsiveness to bar motion declines steeply with time. The most interesting example, however, is that of an increase in responsiveness to noise motion in the face of a simultaneous decrease in responsiveness to bar motion (Fig. 5.3*C*).

The differential variability in response to bar and noise motion is illustrated not because it represents a feature of the present results but because, apart from underlining the necessity of having a record of short-term, trial-to-trial variability, it has important functional implications which will be taken up in Discussion.

CHAPTER 6

DIRECTIONAL TUNING OF CELLS IN AREA 18: A COMPARISON WITH AREA 17

6.1: Influence Of Velocity On The Directional Tuning Of Cells In Area 17 And Area 18 For Motion Of Visual Noise

6.2: Directional Tuning Comparisons For Motion Of Visual Noise, Bar And Spot Stimuli In Cells With Symmetrical, Asymmetrical And Labile Tuning For Bar Motion

6.3: Quantitative Comparisons Of Broadness And Asymmetry Of Directional Tuning For Bar Motion In Area 17 And Area 18 Cells

The present chapter describes results on directional tuning of cells in areas 17 and 18 for motion of a field of static visual noise and for a bar moving against the same stationary noise field as background, with interleaved stimulus presentation. Detailed comparisons of monocular tuning for noise and bar motion were made for the dominant eye receptive field in most cells over a range of velocities. Section 6.1 describes the influence of velocity on directional tuning for noise in area 17 and area 18 cells, classified according to velocity-response functions for bar motion. Section 6.2 is primarily concerned with directional tuning comparisons for noise and bar stimuli in the combined sample of noise-sensitive cells from areas 17 and 18, subdivided according to tuning profile for bar motion. In the most stably-recorded noise-sensitive cells, directional tuning was compared for visual noise, for bars of constant width but differing length, and for single spot stimuli moving at the same velocity. Finally, section 6.3 describes quantitative comparisons of broadness and asymmetry of tuning for bar motion in area 17 and area 18 cells, subdivided according to noise sensitivity, bar tuning profile and cell class.

6.1. INFLUENCE OF VELOCITY ON THE DIRECTIONAL TUNING OF CELLS IN AREA 17 AND AREA 18 FOR MOTION OF VISUAL NOISE

6.1.1. Area 17

Twenty five of the 42 cells recorded in striate cortex were noise-sensitive. Nineteen of these (18 C-cells, 1 B-cell) belonged to Group I and 6 (5 C-cells, 1 S-cell) to Group II (see Chapter 5 for details of classification procedures). Directional tuning for noise was labile and varied with velocity while, with few exceptions (section 6.2.1), tuning for bar motion was velocity-invariant (Hammond and Rock, 1980b; Hammond, 1981; Hammond and Smith, 1983).

At low velocity tuning for noise was typically (22/25 cells) unimodal and skewed away from the preferred direction for bar motion (Figs. 6.1*A* and *E*, 6.3*A* and *E*). With one exception, tuning was broader for noise than for the bar. This is seen particularly clearly in Figs. 6.1*A* and 6.3*A*, which show directional tuning comparisons for the two stimuli in cells sharply tuned for bar motion. Tuning for noise had a less clearly-defined peak and was broader in terms of width at half-height and the range of effective directions of motion. The broader directional tuning for noise might have been anticipated given the known dependence of tuning width on stimulus length (Henry et al., 1974a,b). In this context, it is noteworthy that the single instance of comparable tuning for bar and noise stimuli moving at low velocity reflected exceptionally broad tuning for the bar, rather than unusually narrow tuning for noise.

Differences in directional tuning for noise and bar motion became more pronounced at higher velocities. As velocity was increased, tuning for noise either remained unimodal (5/22 cells), with a shift in preferred direction progressively further away from that for bar motion (Fig. 6.3*A*, *D* and *E*–*H*), or, more commonly (17/22 cells), became bimodal with a trough of depressed response developing, which corresponded to directions most effective for the bar (Fig. 6.1*A*, *D* and *E*–*H*). The degree of bimodality at high velocity varied from a slight inflexion in an otherwise unimodal profile to a complete segregation of the two lobes of tuning. Exceptionally (3/25 cells), noise tuning was strongly bimodal at all velocities used (Fig. 6.2*A*, *D* and *E*–*H*). The two lobes in the bimodal tuning curve could be comparable (Fig. 6.1*C* and *D*) or unequal (Fig. 6.1*G* and *H*; Fig. 6.2*A*, *D* and *E*–*H*) in height and width and were typically, though not necessarily, rather symmetrically displaced in terms of direction about the peak in the tuning profile for bar motion.

For a more detailed analysis of the influence of velocity on directional tuning for noise, and to allow comparison with results from area 18, the sample of noise-sensitive cells in area 17 was subdivided according to velocity-response functions

for bar motion. The small number and narrow range of velocities used (typically 4 velocities up to a maximum of 12 /sec) precluded an accurate derivation of velocity-response functions, and response to bar motion was not explored systematically throughout the velocity bandwidth of most cells. The aim was rather to compare over a range of velocities directional tuning for noise with response to bar motion. Velocity tuned (VT) or velocity high pass (VHP) cells (Orban et al. 1985a) were not encountered among those sensitive to noise in area 17. Indeed they are rare among area 17 cells with receptive fields within 10° of the area centralis projection (Orban et al. 1985a).

(a) Velocity Low-Pass (VLP) Cells

The majority of noise-sensitive cells in area 17 (17/25) responded to bar motion only over a narrow range of slow velocities. Response to the bar was vigorous at the lowest velocity used (typically 1–2 /sec), but declined abruptly as velocity was increased. Upper cut-off velocity lay below or just above the 12 /sec maximum tested. Off-line generation of PSTHs for bar motion in the preferred direction verified that the observed decline in bar response with velocity was not artefactual, due to the use of mean number of impulses per sec as a response measure in deriving directional tuning curves (see Methods). These cells were thus classified as VLP (Orban et al. 1985a). Preferred velocity was frequently higher for noise than for bar motion, and the range of velocities covered was sufficient to conclude that upper cut-off was invariably higher for noise than for bar stimuli. The noise-sensitive S- and B-cells and 13 of the 25 noise-sensitive C-cells had VLP functions for bar motion.

Eleven VLP cells with broad, unimodal tuning for noise at low velocity became progressively more bimodally tuned as velocity was increased. A representative example is illustrated in Fig. 6 (*A*–*D*). At the lowest velocity tested (*A*), tuning for noise was skewed away from the preferred direction for bar motion. Tuning became bimodal at a higher velocity (*B*), with a trough developing in the vicinity

of the peak in bar tuning, which broadened and deepened as velocity was increased further (*C, D*), causing the preferred directions for noise to become more disparate and the lobes of tuning almost completely discrete. In this cell, preferred and upper cut-off velocity were obviously higher for noise than for bar motion, and bimodality of tuning developed at a velocity for which noise evoked maximum response. A few VLP cells, however, developed bimodal tuning below the preferred velocity for noise. In VLP cells whose modality of tuning for noise was velocity-dependent, tuning was strongly bimodal at (and commonly below) the 12 /sec maximum tested, and could persist above upper cut-off velocity for bar motion. In one VLP cell (Fig. 6.2*A–D*), tuning for noise was distinctly bimodal at all velocities used. At the lowest velocity, which was near the optimum for bar motion but below that for noise, two widely-spaced preferred directions for noise were separated by a deep trough of depressed response to motion in directions most effective for the bar. As velocity was increased, the intervening trough remained equally deep but broadened slightly, causing the preferred directions for noise to become more disparate. In VLP cells with bimodal tuning for noise, or in which modality of tuning was velocity-dependent, tuning for noise was broader at high than at low velocity; noise moving in directions outside the tuning profile determined at low velocity became effective when moving at higher velocities.

Three VLP cells were unimodally tuned for noise motion at all velocities used. In Fig. 6.3*A–D*, unimodal tuning persisted above the upper cut-off velocity for bar motion. At low velocity, tuning for noise was skewed away from the preferred direction for the bar. As velocity was increased, the tuning profile for noise shifted progressively further away from the preferred direction for the bar. At the highest velocity tested, response to noise moving in the preferred direction for the bar was negligible, while motion of the bar itself in this direction caused slight suppression of spontaneous activity.

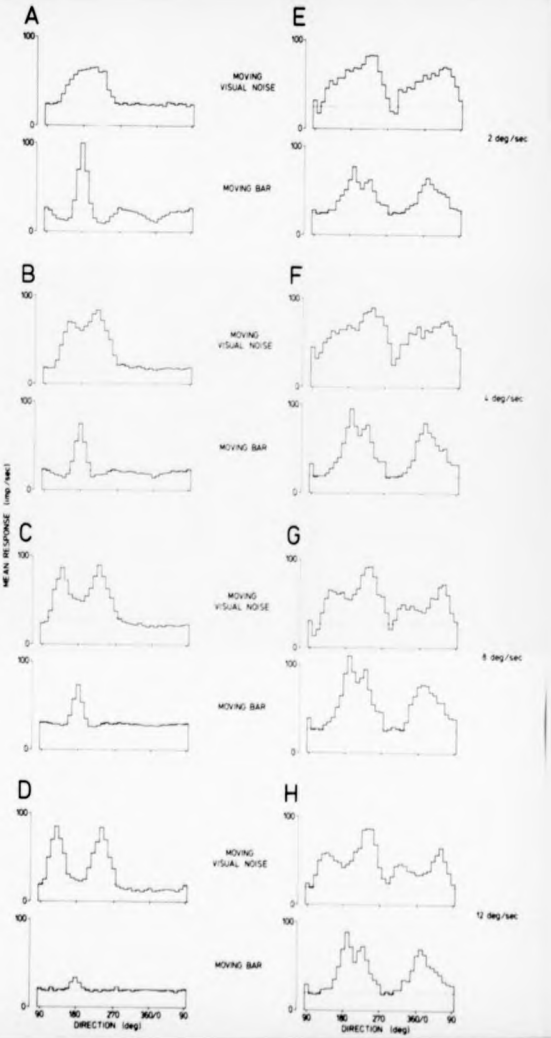

A
B
C
D
E
F
G
H
100
0
MOVING VISUAL NOISE
MOVING BAR
2 deg/sec
4 deg/sec
8 deg/sec
12 deg/sec
MEAN RESPONSE (imp/sec)
90
180
270
360/0
90
DIRECTION (deg)

Fig. 6.1. Directional tuning comparisons for noise and bar motion interleaved, at 4 different velocities, in 2 area 17 Group I C-cells, unimodally tuned for noise at low velocity, but progressively more bimodally tuned as velocity is increased. *A–D*: VLP cell, symmetrically tuned for bar motion. *E–H*: velocity broad band (VBB) cell, asymmetrically tuned for bar motion. Direction stepped in 10° intervals. 4 responses per direction, response expressed as mean number of impulses per sec; spontaneous activity indicated by dotted lines. The 2 pairs of directional tuning curves in each row were derived using the velocity indicated on the extreme right. Note that at a given velocity, bimodality of tuning is more pronounced in the VLP than in the VBB cell (cf. *B*→*F*, *C*→*G*, *D*→*H*). In both cells, preferred direction and broadness of tuning for bar motion are essentially invariant with velocity. Tuning for noise is broader at high than at low velocity. Note the relatively broad tuning for noise at all velocities, particularly in the cell in *A–D*, which features narrow bar tuning, with suppression of firing on both sides of the excitatory profile (most obvious at low velocities), typical of noise-sensitive cells, symmetrically tuned for bar motion (section 6.2.). Note that inhibition is maximal for directions less than 90° from the optimum. Such suppression is absent in *E–H*, which features broad bar tuning characteristic of noise-sensitive cells, asymmetrically tuned for bar motion (section 6.2.). Note the broadening of bar tuning and the consistent secondary peak on the flank closest to the preferred direction for noise, also the comparably broad and asymmetrical bar tuning for opposite directions of motion (section 6.2.). At a given velocity, modality of tuning for noise is consistent for opposite directions of motion, at high velocity the profile for noise has 4 lobes, 2 associated with each direction of bar motion. The cell in *A–D* is direction-selective, both for noise and for bar motion, with suppression of firing in the null direction whose magnitude is velocity-dependent for each stimulus. Note that the velocity-dependent changes in magnitude of null suppression do not occur in parallel for the 2 stimuli, also that null-suppression caused by bar motion is maximum for directions opposite those which evoke the strongest excitatory response. Note that in the VLP cell (*A–D*) preferred velocity is clearly higher for noise than for bar motion.

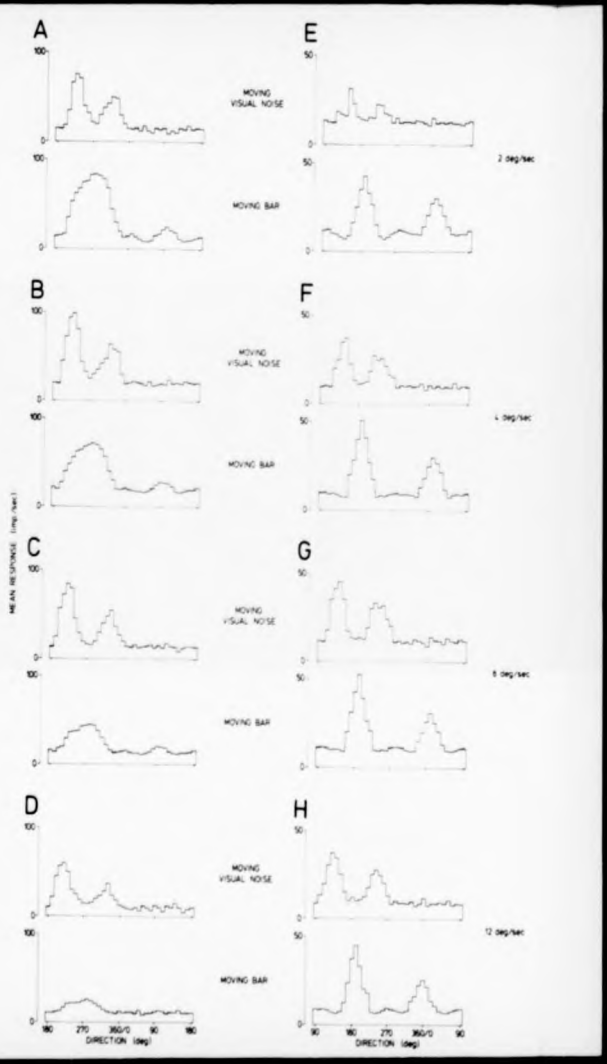

A
B
C
D
E
F
G
H
MOVING VISUAL NOISE
MOVING BAR
2 deg/sec
4 deg/sec
8 deg/sec
12 deg/sec
MEAN RESPONSE (imp/sec)
DIRECTION (deg)
180
270
360/0
90
180

Fig. 6.2. Directional tuning comparisons for noise and bar motion interleaved, at 4 different velocities, in 2 area 17 Group I C-cells with bimodal tuning for noise. Conventions, derivation and layout as in Fig. 6.1. *A–D* VLP cell, asymmetrically tuned for bar motion. *E–H* VBB cell, symmetrically tuned for bar motion. Note that tuning for noise is bimodal in *A–D* near the preferred velocity for bar motion and below that for noise motion, and in *E–H*, throughout the range of preferred velocities for bar motion and well below the optimum velocity for noise motion. Noise tuning remains bimodal at all velocities tested, but is broader at high than at low velocities. Preferred direction and broadness of tuning for bar motion are essentially invariant with velocity. In both cells, the lobes of tuning for noise are unequal in height. While in *A–D* the profile for bar motion is asymmetrical, with broader tuning on the flank closest to the preferred direction for noise, in *E–H* bar tuning is symmetrical with suppression of firing on both sides of the excitatory profile, which is maximum for directions less than 90° from the optimum (section 6.2). Suppression is apparent on the sides of both excitatory profiles for the bar (corresponding to opposite directions of motion), which are equally narrow and symmetrical at all velocities. In the asymmetrically tuned cell, such suppression is present only for motion in the non-preferred direction, in the absence of a response to noise (section 6.2). Note that in the VLP cell (*A–D*), preferred velocity is higher for noise than for bar motion.

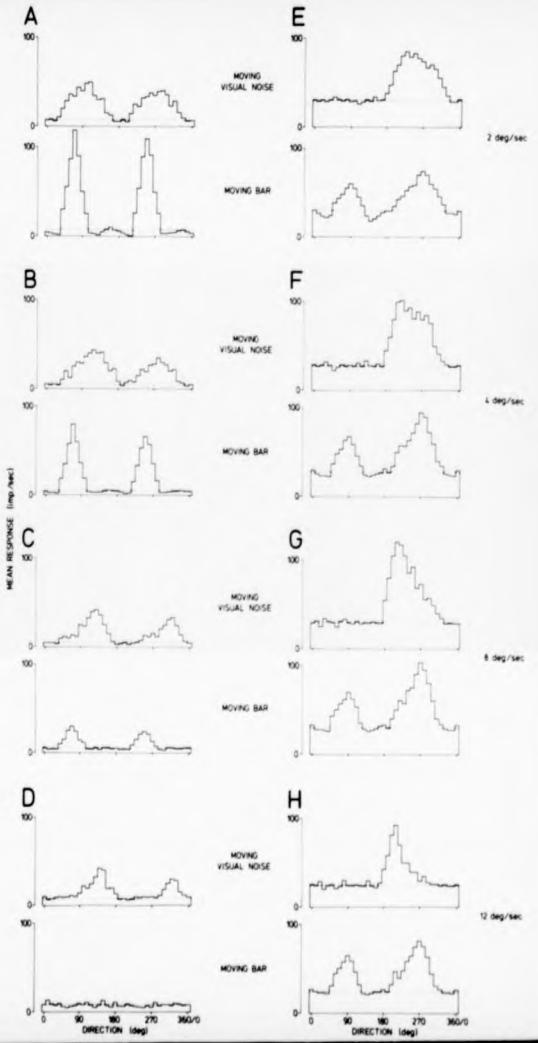

A
B
C
D
E
F
G
H
100
0
MOVING VISUAL NOISE
MOVING BAR
2 deg/sec
4 deg/sec
8 deg/sec
12 deg/sec
MEAN RESPONSE (imp/sec)
0
90
180
270
360/0
DIRECTION (deg)

Fig. 6.3. Directional tuning comparisons for bar and noise motion interleaved, at 4 different velocities, in 2 area 17 C-cells with unimodal tuning for noise. Conventions, derivation and layout as in Fig. 6.1. *A–D* Group II VLP cell, symmetrically tuned for bar motion. *E–H* Group I VBB cell, asymmetrically tuned for bar motion. At low velocity, tuning for noise is relatively broad and skewed away from the preferred direction for the bar. Note particularly in *A–D*, that as velocity is increased the profile for noise shifts progressively further away from the preferred direction for bar motion. Preferred direction and broadness of tuning for the bar are essentially invariant with velocity. In *A–D*, bar tuning is equally narrow and symmetrical for opposite directions of motion, with suppression of firing on both sides of each excitatory profile (corresponding to opposite directions of motion), which is maximal for directions less than 90° from the optimum (section 6.2.). In *E–H*, the profile for bar motion in the preferred direction is asymmetrical, with broader tuning on the flank closest to the preferred direction for noise. In the non-preferred direction, in the absence of a response to noise, bar tuning is narrower and more symmetrical, with suppression of firing on both sides of the excitatory profile (section 6.2.). Note that in *A–D*, tuning for noise remains unimodal beyond the upper cut-off velocity for bar motion.

(b) Velocity Broad-Band (VBB) Cells

The remaining 10 noise-sensitive cells in area 17 gave a response to bar motion of comparable strength over the range of velocities used (typically 2–12 /sec) and were classified as velocity broad-band (VBB; Orban et al. 1981a). Upper cut-off velocity clearly lay well beyond the maximum 12 /sec tested, while qualitative testing established that response to bar motion did not decline substantially at velocities below those used for deriving directional tuning curves. While VLP cells were predominant among noise-sensitive C-cells with central receptive fields (< 1°), VBB cells were more common (7 : 12) among those with receptive fields in the range 2–10°.

VLP and VBB cells showed comparable alterations in tuning for noise with change in velocity. Thus, the majority of VBB cells (7 : 9) were unimodally tuned for noise at low velocity, but became progressively more bimodally tuned as velocity was increased: a trough of depressed response to noise moving in directions optimal for the bar separated two progressively more widely disparate preferred directions. There were, however, two important differences between VLP and VBB cells with velocity-dependent modality of tuning for noise. First, in VBB cells tuning became bimodal at velocities for which bar motion evoked the maximum or near maximum response (Fig. 6.1*G*), whereas in VLP cells bimodality in tuning developed when the bar response was on the decline (Fig. 6.1*B*). Second, at a given velocity, VLP cells were characteristically more strongly bimodally tuned for noise than were VBB cells (compare in Fig. 6.1 *B* with *F*, *C* with *G*, *D* with *H*). Indeed in one VBB cell, the tuning profile for noise showed no more than a slight inflexion at the 12 /sec maximum tested. Only one VBB cell had two discrete lobes of tuning for noise moving at high velocity, typical of VLP cells. This was one of the two VBB cells in which tuning was distinctly bimodal at the lowest velocity used, well below the preferred velocity for noise (Fig. 6.2*E*, *H*). In VBB cells with bimodal tuning for noise, or in which modality of tuning was velocity-dependent, noise tuning was frequently broader at high than at low velocities.

Directional tuning comparisons for noise and bar motion in the remaining VBB cell are shown in Fig. 6.3E–H, in which it can be seen that tuning for noise was unimodal at all velocities tested. Preferred directions for noise and bar motion were dissimilar at the lowest velocity used, well below the optimum velocity for noise, though differences in tuning for bar and noise stimuli became more pronounced as velocity was increased.

6.1.2. Area 18

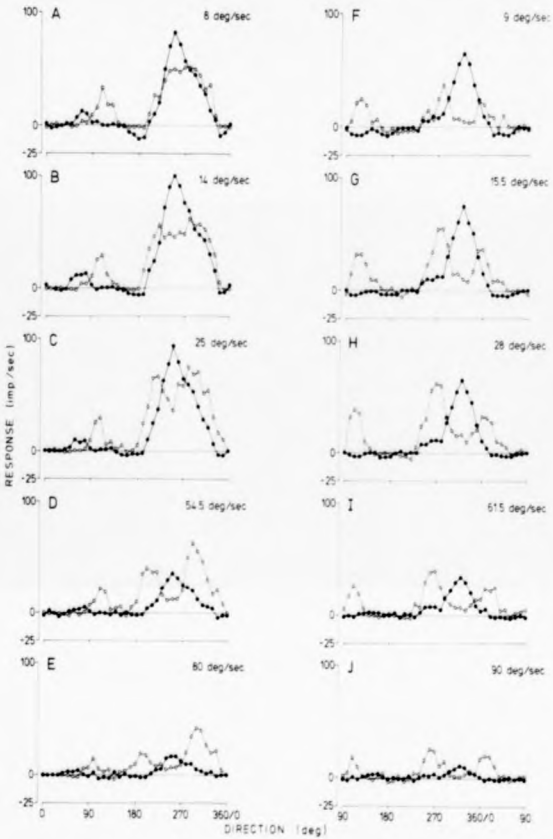
Of the 68 cells recorded in area 18, 30 were noise-sensitive. Twenty-two of these (20 C-cells, 1 B-cell and 1 S-cell) belonged to Group I, and 8 (4 C-cells, 3 B-cells and 1 S-cell) to Group II. As in area 17, directional tuning for noise was labile and varied with velocity in every cell. In considering the influence of velocity on directional tuning for noise, the sample of area 18 cells was subdivided according to velocity-response functions for bar motion. Directional tuning curves for area 18 cells, in which response was expressed as peak firing frequency, yielded a realistic measure of bar response at different velocities. However, since directional tuning comparisons in each cell were made at a maximum of five velocities, typically over a ten-fold range, precise velocity-response curves for bar motion could not be derived. The number and range of velocities covered, however, was sufficient to classify most noise-sensitive cells in area 18 as VBB, VT or VHP (Orban et al. 1984a). VLP cells were not encountered in area 18, and indeed they are virtually absent in this area (Orban et al. 1984a). In 4 cells, the number of velocities at which directional tuning curves were derived was insufficient for unequivocal assignment to one of the above classes.

(a) Velocity Broad-Band (VBB) Cells

VBB cells in area 18 responded to bar motion over a wide range of velocities but had no clear optimum velocity. Since stimulus excursion always exceeded minimum response field width and maximum sweep time was [illegible], responses

to very slow velocities could not be tested quantitatively. VBB cells responded vigorously to bar motion at the lowest velocity used for deriving directional tuning curves (7–10°/sec), and qualitative testing established that the response did not decline substantially at lower velocities. Response remained rather constant up to 25–40°/sec, but declined steeply thereafter. Thus in the present samples, there was some indication that VBB cells in area 18 had a wider range of preferred velocities than their counterparts in area 17. This may reflect the receptive field eccentricities at which VBB cells were encountered in the two areas: no VBB cell in area 17, but almost half of those in area 18 had receptive fields more than 10° from the area centralis projection. Although most VBB cells responded both to bar and to noise motion at the highest velocity used, the range of velocities covered was sufficient to conclude that upper cut-off was characteristically higher for noise than for bar motion.

Of the 10 VBB cells recorded in area 18, 8 showed broad, unimodal tuning for noise at low velocity. One of these was unimodally tuned at all velocities used (not illustrated), while in the remaining 7 cells, tuning became progressively more bimodal as velocity was increased, with progressive separation of the two peaks and deepening of the intervening trough (Fig. 6.4*A–E*). These cells were more broadly tuned for noise at high than at low velocities. Bimodality of tuning developed at one of the preferred velocities for bar motion, and frequently below the velocity optimum for noise, but was most pronounced at high velocities when the response to both stimuli was on the decline. In all but one VBB cell with velocity-dependent modality of tuning, the profile for noise moving at velocities near 12°/sec (the highest velocity used for deriving tuning curves in area 17 cells) showed only a slight inflexion in the vicinity of the peak in bar tuning (Fig. 6.4*B*). The exception was unimodally tuned for noise at 12°/sec, but bimodally tuned at higher velocities. Thus VBB cells in area 18 became strongly bimodally tuned for noise at higher velocities than their counterparts in area 17 (compare Figs. 6.4*A–E* and 6.1*E–H*), and at much higher velocities than VLP cells in area 17 (compare Figs. 6.4*A–E* and 6.1*A–D*).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F
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B
14 deg/sec
G
15.5 deg/sec
C
25 deg/sec
H
28 deg/sec
D
54.5 deg/sec
I
61.5 deg/sec
E
80 deg/sec
J
90 deg/sec
100
0
-25
RESPONSE (imp/sec)
0
90
180
270
360/0
DIRECTION (deg)

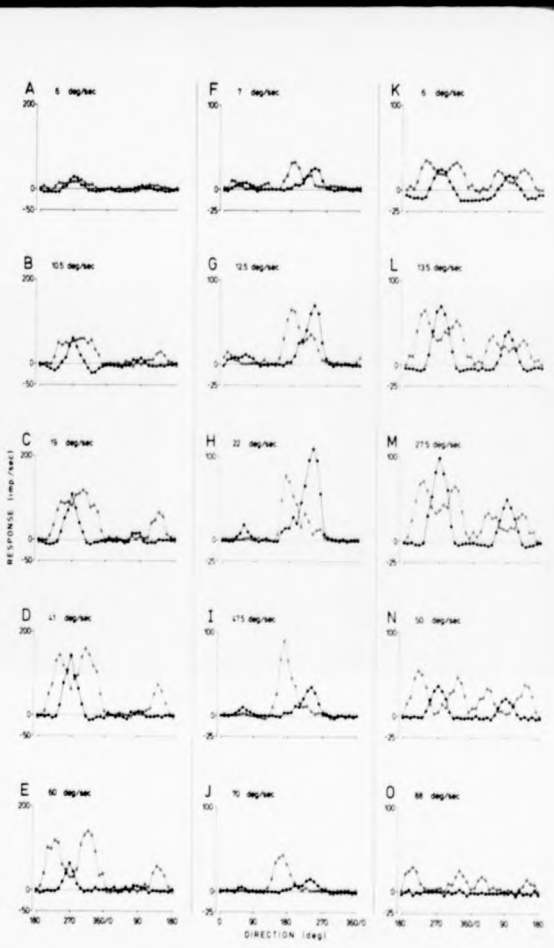
Fig. 6.4. Directional tuning comparisons for bar and noise motion interleaved (solid and broken lines respectively), at 5 different velocities, in each of 2 area 18 VBB Group 1 C-cells (*A–E* and *F–J*). Direction stepped in 10° intervals. Response magnitude derived from PSTHs (4 responses per direction) and expressed as peak firing frequency (averaged over 3 adjacent bins centred on the bin containing the highest spike count) subtracted from the mean spontaneous activity (thin continuous horizontal lines) assessed at the time each PSTH was compiled. In *A–E* tuning for noise is unimodal at low velocity but becomes progressively more bimodal as velocity is increased. Note that bimodality in tuning for noise develops at one of the preferred velocities for bar motion and below the optimum velocity for noise, but is most pronounced at higher velocities when the response to both stimuli is on the decline. Tuning for bar motion is asymmetrical: preferred direction and broadness of tuning being essentially invariant with velocity. The major lobe in the bimodal tuning curve for noise moving at high velocity (*D*, *E*) coincides with the broader flank of bar tuning (section 6.2.c). In *F–J*, noise tuning is distinctly bimodal at all velocities, and below the optimum velocity for noise. The two lobes of tuning for noise are unequal in strength. Tuning for the bar is symmetrical in terms of half-width at half-height, but has a drawn-out tail to the left of the peak, which coincides with the major lobe of noise tuning (section 6.2.). Note in both cells the broader tuning for noise at high than at low velocities, the dissimilar tuning profiles for noise moving in opposite directions, and the broad directional tuning for bar motion characteristic of noise-sensitive cells with asymmetrical bar tuning.

Two VBB cells were strongly bimodally tuned for noise at all velocities used, and thus throughout the range of preferred velocities for bar motion. One of these is shown in Fig. 6.4*E–J*, in which it can be seen that tuning was distinctly bimodal well below the preferred velocity for noise, though the two peaks became slightly more disparate as velocity was increased.

(b) Velocity Tuned (VT) Cells

Eleven noise-sensitive cells recorded in area 18 were classified as VT. Response to bar motion declined steeply on both sides of the optimum velocity. Velocity optima ranged from 16–41°/sec, though the small number of velocities at which directional tuning curves were derived precluded a precise determination of preferred velocity. That VT cells with lower preferred velocities (Orban et al., 1981a) were not encountered among noise-sensitive cells in area 18 may be partially due to the fact that the majority (9/11) had receptive fields more than 5° from the area centralis projection, for the optimum velocity of tuned cells increases with receptive field eccentricity (Orban et al., 1981a). Even for measurements made at a small number of velocities, some VT cells had obviously higher preferred velocities for noise than for bar motion (Fig. 6.3*F*, *I*). Others showed a steeper decline in response to bar than to noise motion as velocity was increased above the optimum. Although most VT cells gave some response to both stimuli at the highest velocity tested, the number and range of velocities covered was sufficient to conclude that upper cut-off was invariably higher for noise than bar motion.

Six VT cells had broad, unimodal tuning for noise at low velocity. Five of these became progressively more bimodally tuned as velocity was increased. A typical example is shown in Fig. 6.5*A–E*, in which it can be seen that tuning for noise developed a slight inflexion below the optimum velocity for bar and for noise motion (*C*), was unequivocally bimodal at the preferred velocity for the bar (*D*), but more strongly bimodal at the highest velocity used (*E*) when the bar response was on the decline. In a high proportion (5/11) of VT cells, tuning for noise was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B 10.5 deg/sec
C 15 deg/sec
D 21 deg/sec
E 60 deg/sec
F 7 deg/sec
G 12.5 deg/sec
H 22 deg/sec
I 47.5 deg/sec
J 70 deg/sec
K 6 deg/sec
L 13.5 deg/sec
M 27.5 deg/sec
N 50 deg/sec
O 88 deg/sec
RESPONSE (imp/sec)
DIRECTION (deg)

Fig. 6.5. Directional tuning comparisons for bar and noise motion interleaved at 3 different velocities, in each of 3 area 18 VT Group I cells (*A–E*, *F–J*, *K–O*). Conventions and derivation as in Fig. 6.4. In *A–E* tuning for noise is unimodal at low velocity, but becomes progressively more bimodal as velocity is increased. Note that bimodality of tuning develops below the optimum velocity for bar and for noise motion. In *F–J* tuning for noise is unimodal and preferred directions for noise and bar motion are radically dissimilar at all velocities. Tuning for noise is asymmetrical at low-to-medium velocities (with broader tuning on the flank closest to the preferred direction for the bar), but much more symmetrical at high velocities. Note the shift with velocity in the profile for noise progressively further away from the preferred direction for the bar. Preferred direction and broadness of tuning for bar motion are essentially invariant with velocity. The tuning profile is asymmetrical with broader tuning on the flank closest to the preferred direction for noise (section 6.2.). In *K–O* tuning for noise is bimodal at the lowest velocity used, below the preferred velocity for bar and for noise motion. Bimodality of tuning becomes more pronounced as velocity is increased and persists above cut-off velocity for the bar. In *A–E* and *K–O*, bar tuning is symmetrical, preferred direction and broadness of tuning being essentially invariant with velocity. Note the narrow bar tuning and suppression of firing on both sides of the excitatory profile (section 6.2.). In *K–O* the tuning profiles corresponding to preferred and opposite directions of bar motion are equally narrow and symmetrical at all effective velocities. Tuning for noise has 4 lobes, 2 associated with each direction of bar motion. In contrast, note that in *A–D* modality of tuning for noise is different for opposite directions of motion. The cell in *F–J* gives a negligible response to bar motion in the non-preferred direction, but at high velocities is completely direction-selective for noise. Null-suppression would not have been apparent in this cell, since it lacked spontaneous activity.

bimodal at the lowest velocity tested (0.5°/sec). In one of these, the two lobes of tuning for noise were almost completely discrete throughout the range of velocities used. In others, of which a representative example is shown in Fig. 6.5K–O, tuning was distinctly bimodal at the lowest velocity tested, but more strongly bimodal at high velocities when the response to the bar was on the decline. Indeed this cell had two discrete lobes of tuning for noise, with widely disparate peaks, above the upper cut-off velocity for bar motion (Oc). The intervening trough of depressed response to noise spanned the range of directions for which the bar evoked excitation when moving at lower velocities.

Directional tuning comparisons for the remaining VT cell are shown in Fig. 6.5F–J, in which it can be seen that tuning for noise remained essentially unimodal at all velocities, although there was a slight, consistent inflexion (at 210°) in the profile determined at low velocities (F, H). Preferred directions for noise and bar motion were radically dissimilar at the lowest velocity used, below the optimum for the bar and well below that for noise. With increase in velocity, the profile for noise shifted progressively further away from the preferred direction for bar motion. It was distinctly asymmetrical at low velocities, with broader tuning on the flank closest to the preferred direction for the bar, but more symmetrical at higher velocities.

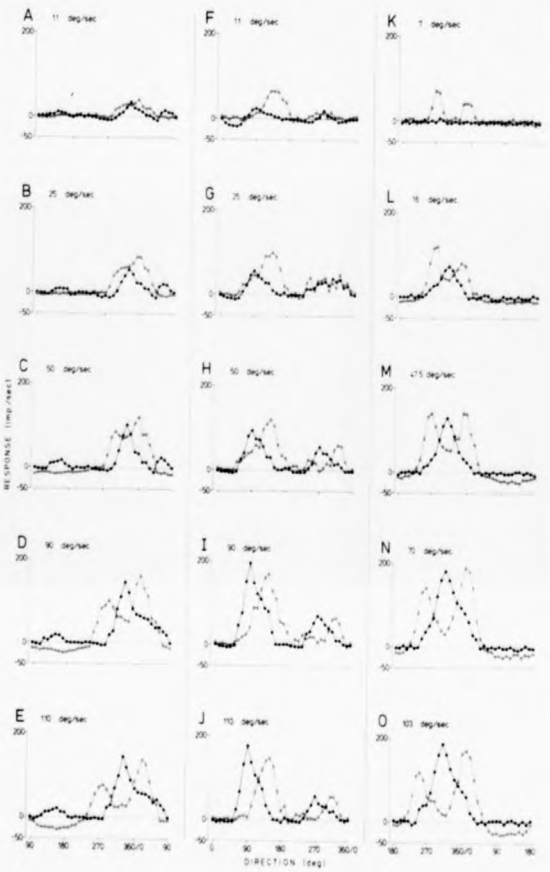
(c) Velocity High-Pass (VHP) Cells

Only 5 noise-sensitive cells in area 18 had VHP functions for bar motion. Bar response was weak or absent at the lowest velocity tested, increased with velocity up to some maximum value, and remained relatively constant thereafter. The low proportion of VHP cells among those sensitive to noise could be attributed primarily to the receptive field eccentricities of noise-sensitive cells recorded in area 18. VHP cells are associated with the C- and A families (Orban et al. 1981a). A-cells however were recorded infrequently and were noise-insensitive. The majority of noise-sensitive C-cells had receptive fields within 10° of the area centralis projec-

tion, whereas VHP cells are rare in area 18 subserving central vision (Orban et al. 1985a). They are the predominant cell type among cells with receptive fields more than 10° from the area centralis projection, where the receptive fields of only 3 noise-sensitive C-cells lay, two of these had VHP functions. Moreover, according to Orban et al. (1985a), VHP cells in area 18 are encountered predominantly in the superficial layers, while in the present sample of noise-sensitive C-cells those from the deep layers were in the majority. As far as could be ascertained from measurements made at a limited number of velocities, the velocity-response functions and saturation velocities were similar for noise and bar motion in all VHP cells.

In two VHP cells, tuning for noise was broad and unimodal at low velocity, but became progressively more bimodal as velocity was increased, with progressive separation of the two preferred directions and deepening of the intervening trough (Fig. 6.6*A–E*). Bimodality of tuning developed at a higher velocity in these cells than in all others whose modality of tuning was velocity-dependent, but well below the velocity which evoked the maximum response. Two VHP cells were bimodally tuned for noise at all velocities used. The most interesting VHP cell was strongly bimodally tuned for noise below the velocity threshold for bar motion (Fig. 6.6*K–O*). At low velocity (*K*), two widely spaced, discrete lobes of tuning for noise were separated by a trough corresponding to the most effective directions for the bar when moving at higher velocities. However, the relative response to noise moving in the preferred direction for the bar (compared with the maximum response) improved at intermediate velocities (*L, M*), and only as velocity was increased further (*N, O*), did the intervening trough broaden and deepen, causing the two preferred directions to become more disparate. Bimodality in tuning was thus most pronounced at low and at high velocities. In VHP cells with bimodal tuning for noise, or in which modality of tuning was velocity-dependent, tuning for noise was broader at high than at low velocity.

The remaining VHP cell had a single preferred direction for noise which was rad-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K 7 deg/sec
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G 25 deg/sec
L 16 deg/sec
C 50 deg/sec
H 50 deg/sec
M 175 deg/sec
D 90 deg/sec
I 90 deg/sec
N 70 deg/sec
E 110 deg/sec
J 110 deg/sec
O 103 deg/sec
200
0
-50
RESPONSE (imp/sec)
90 180 270 360/0 90
0 90 180 270 360/0
180 270 360/0 90 180
DIRECTION (deg)

Fig. 6.6. Directional tuning comparisons for bar and noise motion interleaved, at 5 different velocities in each of 3 VRP Group I Ccells. Conventions and derivation as in Fig. 6.4. In *A-E* tuning for noise is unimodal at low velocity, but becomes progressively more bimodal as velocity is increased. Note that tuning is strongly bimodal well below the preferred velocity for bar and noise motion. The cell in *F-J* has a unique preferred direction for noise which is radically different from that for the bar at all velocities. Preferred direction and broadness of tuning for bar motion are essentially invariant with velocity, the profile being asymmetrical with broader tuning on the flank closest to the preferred direction for noise (section 6.2.). The profile for noise is asymmetrical at low-to-medium velocities (with broader tuning on the flank closest to the preferred direction for the bar), but rather symmetrical at high velocity. In *K-O*, directional tuning is strongly bimodal below the threshold velocity for bar motion, and well below the preferred velocity for noise. Bimodality of tuning obtains at all velocities, but is most pronounced at low and high velocities. In *A-E* and *K-O* directional tuning for bar motion is labile. Note the variation with velocity in the tuning profile for the bar and its association with velocity-dependent changes in tuning for noise (section 6.2.), also the velocity-dependent changes in magnitude of null suppression for noise. All 3 cells have similar velocity response functions and preferred velocities for noise and for bar motion.

ically different from that for the bar at all velocities used (Fig. 6.6*F–J*). At low-to-medium velocities (*F–H*), the profile for noise was asymmetrical with broader tuning on the flank closest to the preferred direction for the bar. At high velocity (*J*), the response to noise moving in the preferred direction for the bar was negligible and tuning was much more symmetrical.

(d) Unclassified Cells

In 4 noise-sensitive cells in area 18, the number of velocities at which directional tuning curves were derived was too small to allow unambiguous classification on the basis of velocity-response functions. In 3 of these, tuning for noise was unimodal at the lowest velocity used, but became bimodal as velocity was increased, in the face of an improvement in response both to bar and to noise motion.

6.1.3. Directional Bias For Noise And For Bar Motion

Thirty-three of the 55 noise-sensitive cells in areas 17 and 18 gave a response to bar motion in opposite directions along a common axis, though in 14 of these the response to bar motion in the non-preferred direction was negligible. Eight cells in the latter group (Figs. 6.2*A, D*; 6.6*A, E*) and 5 of 12 cells directionally biased for bar motion (Figs. 6.2*E, H*; 6.3*E, H*) were *completely direction-selective for noise*. Eight of these showed suppression of firing to noise moving in the non-preferred (null) direction; the magnitude of null-suppression was velocity-dependent. The remaining 20 cells were *direction-biased* or *bidirectional for noise*. In eleven of these, modality of tuning for noise at a given velocity was consistent for opposite directions of motion, i.e., a single lobe or a pair of lobes associated with each direction of bar motion. Modality of noise tuning either remained constant with velocity (Figs. 6.3*A, D*; 6.5*K, O*) or was velocity-dependent, with the transition from unimodal to bimodal tuning occurring at the same velocity for opposite directions of motion (Fig. 6.1*E, H*). In 9 cells, modality of noise tuning was different

for opposite directions of motion, at least at some velocities. Typically, in the preferred direction, unimodal tuning for noise gave way to bimodal tuning as velocity was increased, while in the non-preferred direction, tuning remained unimodal at all velocities (Figs. 6.4*A, E*; 6.7*A, E*).

Twenty-two noise-sensitive cells were completely direction-selective for bar motion (10 with null suppression). Sixteen of these were, in addition, *completely direction-selective for noise* (15 with null suppression). Six cells showed suppression of firing to noise, but not to the bar, moving in the non-preferred direction (Figs. 6.6*K, O*; 6.8*A, D*), while both stimuli evoked null suppression in 9 cells (Figs. 6.1*A, D*; 6.8*E, I*). The presence or absence and magnitude of null suppression was velocity-dependent for each stimulus. For the bar, it was strongest at velocities for which motion in the preferred direction evoked the maximum response (Fig. 6.1*A, D*). This was also generally the case for noise (Fig. 6.6*K, O*; Fig. 6.8*A, D* and *E, I*), though in some cells magnitude of null suppression seemed to be associated with the total area under the directional tuning curve, rather than with the response to motion in the preferred direction. The velocity-dependent changes in magnitude of null-suppression frequently did not occur in parallel for noise and for bar motion. Exceptionally, the influence of velocity on magnitude of null-suppression was opposite for the two stimuli (Fig. 6.1*A, D*). For the bar, null-suppression was commonly maximal for motion in directions opposite those which evoked the best excitatory response (Fig. 6.1*A, D*). Six cells completely direction-selective for bar motion were *directionbiased or bidirectional for noise*. In 3 of these, modality of tuning for noise moving at high velocities was different for opposite directions of motion (Fig. 6.4*F, I*).

6.2. DIRECTIONAL TUNING COMPARISONS FOR MOTION OF VISUAL NOISE, BAR AND SPOT STIMULI IN CELLS WITH SYMMETRICAL, ASYMMETRICAL AND LABILE TUNING FOR BAR MOTION

For detailed comparisons of directional tuning for motion of noise, bar and single spot stimuli, the sample of noise-sensitive cells was subdivided according to directional tuning profile for bar motion. Preferred direction and half-widths of tuning at half-height were determined where appropriate by approximating the flanks of tuning with two straight lines fitted by eye (Hammond and Andrews, 1978). This procedure proved particularly suitable for narrowly tuned cells, but in many others provided a poor fit to the data. Some cells were rather symmetrically tuned in terms of tuning. In addition, even though the grain of tuning was coarse in the present determinations (10°), the tuning profiles for bar motion in many cells had decidedly rounded peaks. This was not due to response saturation, since similar bar tuning profiles obtained when tuning curves were compiled at non-optimal velocities. Thus, straight lines were fitted to the data points when the fit was good, but otherwise smooth curves were fitted by eye (DeValois et al., 1982).

6.2.1. Distribution Of Noise-Sensitive Cells With Symmetrical, Asymmetrical And Labile Bar Tuning In Areas 17 And 18

A break-down of noise-sensitive cells in areas 17 and 18, according to bar tuning profile is given in Table 6.1, in which it can be seen that almost one half were asymmetrically tuned. Asymmetrically tuned cells had at all velocities a ratio of half-widths at half-height greater than 1.2 (Figs. 6.1*E, H*; 6.2*A, D*; 6.3*E, H*; 6.4*A, E*; 6.5*F, J*; 6.6*F, J*) or a drawn-out tail on one flank of tuning (Fig. 6.4*F, J*). Fewer than a third of noise-sensitive cells were symmetrically tuned for bar motion at all velocities. In approximately a quarter, bar tuning was labile and varied

	SYMMETRICAL	ASYMMETRICAL	LABILE	
AREA 17				
GROUP I	3 (16)	11 (58) [1B]	5 (26)	19
GROUP II	5 (83) [1S]	1 (17)	-	6
	8 (32)	12 (48)	5 (20)	25
AREA 18				
GROUP I	4 (18) [1B]	9 (41) [1S]	9 (41)	22
GROUP II	5 (62.5) [2B, 1S]	3 (37.5) [1B]	-	8
	9 (30)	12 (40)	9 (30)	30
TOTAL	17 (31)	24 (44)	14 (25)	55

Table 6.1. Distribution of Group I and Group II (noise-sensitive) cells in areas 17 and 18 according to directional tuning profile for bar motion. (See text for definition of symmetrical, asymmetrical and labile bar tuning). The great majority of cells belong to the C family; numbers of S- and B-cells are indicated in square brackets. Figures in parentheses are percentages of totals in the right-hand column.

with velocity. The proportions of cells in areas 17 and 18 with symmetrical, asymmetrical and labile bar tuning were broadly similar. In both areas, only Group I C-cells had labile tuning for bar motion. Cells with labile bar tuning formed a higher proportion of Group I cells in area 18 than in area 17, though this difference was not statistically significant. Areas 17 and 18 contained an almost identical proportion of noise-sensitive cells with symmetrical bar tuning, though many of those in area 18 belonged to the B- and S families. Group II contained a significantly higher proportion of cells with symmetrical bar tuning (71%) than did Group I (17%) (Chi-squared, $P < 0.001$). Noise-sensitive, asymmetrically tuned cells belonged predominantly (83%) to Group I, though the difference in the proportions of Group I (40%) and Group II (2%) cells with asymmetrical bar tuning did not reach statistical significance. However among cells with velocity invariant bar tuning, those with asymmetrical and those with symmetrical tuning were predominant in groups I and II respectively; these differences were statistically significant (Chi-squared, $P < 0.02$).

6.2.2. Directional Tuning Comparisons In Noise-Sensitive Cells For Motion Of Visual Noise, Bar And Spot Stimuli

The results on directional tuning comparisons for noise, bar and single spot stimuli in area 17 and area 18 cells were broadly similar and will be described together.

(a) Symmetrically Tuned Cells

Noise-sensitive, symmetrically tuned cells had conspicuously narrow directional tuning for bar motion (section 6.3, Table 6.2). In spontaneously active cells, suppression of firing was seen on both sides of the excitatory profile (Figs. 6.1A, D, 6.2E, H, 6.3A, D, 6.5A, E, 6.5K, O, 6.7A). Inhibition was commonly maximal for directions less than 90° from the optimum, and typically most pronounced at low velocities. Tuning was broader for noise than for bar motion at all velocities. Thus, a feature of directional tuning comparisons in symmetrically tuned cells was

the excitation evoked by noise moving in directions for which bar motion caused inhibition. Noise-sensitive cells with symmetrical bar tuning could be unimodally (Fig. 6.3*A–D*) or bimodally (Figs. 6.2*E–H*, 6.5*K–O*) tuned for noise at all velocities used, or alternatively, unimodal tuning at low velocity could give way to bimodal tuning as velocity was increased (Figs. 6.1*A–D*). When noise tuning was bimodal the two lobes could be comparable (Figs. 6.1*C* and *D*, 6.5*D* and *E*) or unequal (Fig. 6.2*E–H*) in strength. The suppression of spontaneous activity on both sides of the excitatory profile was usually weak or absent at right angles to the preferred direction. Occasionally a small secondary peak was seen in this region, which did not seem to be related to the tuning profile for noise; it was sometimes present outside the range of effective directions for noise (Fig. 6.7*A*) and was seen in some symmetrically tuned cells which were insensitive to noise.

In 8 noise-sensitive, symmetrically tuned cells (3 in area 17, 5 in area 18) in which directional tuning comparisons for noise and bar motion had been made over a range of velocities, tuning curves were derived in addition, for motion of visual noise and single spot stimuli interleaved. Tuning curves were compiled using a velocity at which preferred directions for noise and bar motion were radically dissimilar. In Fig. 6.7*A*, B, which shows directional tuning comparisons for noise, bar and spot stimuli moving at 8 °/sec in an area 17 Group I Cell lacking substantial length summation, noise tuning was bimodal, with two peaks of unequal height separated by a trough of depressed response spanning the range of response directions for the bar. Bar tuning was narrow, with suppression of firing on both sides of the excitatory profile. Such suppression was absent in the tuning profile for the spot, which was substantially broader than that for the bar. The preferred directions for the two stimuli were, however, the same. Comparable results obtained in all 8 noise-sensitive, symmetrically tuned cells in which the above comparisons were made, including those unimodally tuned for noise, and those bimodally tuned with lobes of similar strength. Cells showing substantial length summation had similar preferred directions for spot and bar motion, but the peak in tuning for the spot was less well-defined than in cells lacking length summation.

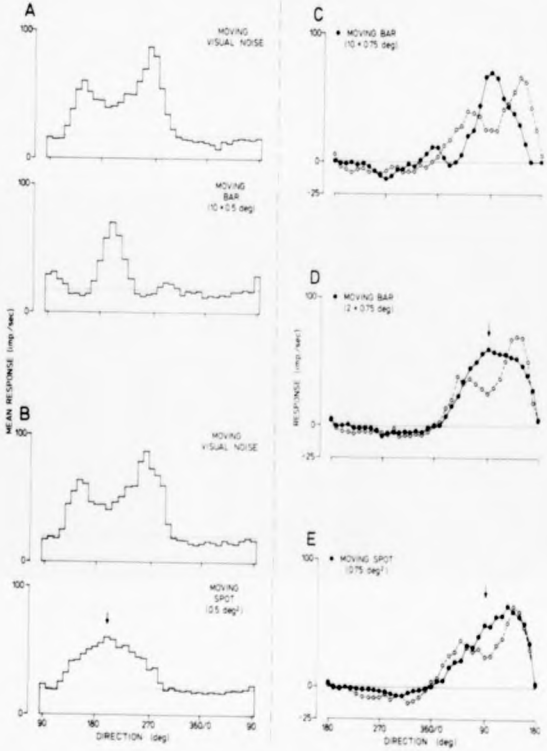
A
MOVING VISUAL NOISE
MOVING BAR (10 × 0.5 deg)
B
MOVING VISUAL NOISE
MOVING SPOT (0.5 deg²)
MEAN RESPONSE (imp/sec)
DIRECTION (deg)
C
MOVING BAR (10 × 0.75 deg)
D
MOVING BAR (2 × 0.75 deg)
E
MOVING SPOT (0.75 deg²)
RESPONSE (imp/sec)
DIRECTION (deg)

Fig. 6.7.

A–B Comparison of directional tuning for visual noise, and for bar and single spot stimuli (dimensions in parentheses), in the same area 17 noise-sensitive C-cell with symmetrical tuning for bar motion and lacking substantial length summation. Minimum response field length, 2·8°. Simultaneously-derived pairs of directional tuning curves for noise and bar motion (*A*) and for noise and spot motion (*B*) with interleaved presentation of each stimulus in a pair. Direction stepped in 30° intervals, 4 responses per direction, response expressed as mean number of impulses per sec, spontaneous activity indicated by dotted lines, velocity 8°/sec. Arrow in *B* indicates the preferred direction of the same cell for bar motion (*A* lower function). Note that tuning is broader for the spot than for the bar, but that preferred directions for the two stimuli are similar, and radically different from the preferred direction for noise.

C–E Comparison of directional tuning for motion of visual noise (broken lines in each function) and for bars of constant width but different length (solid lines; dimensions in parentheses) in the same area 18 Group I C-cell with asymmetrical tuning for motion of a long bar, and lacking substantial length summation. Minimum response field length, 0·2°. Direction stepped in 30° intervals. Response magnitude derived from PSTHs (4 responses per direction) and expressed as peak firing frequency (averaged over 3 adjacent bins centred on the bin containing the highest spike count), subtracted from the mean spontaneous activity (thin, continuous horizontal lines) assessed at the time each PSTH was compiled. Simultaneously-derived pairs of directional tuning curves for moving visual noise interleaved with motion of a long bar (*C*), a short bar (*D*), and a spot (*E*). Each pair of tuning curves was derived using the same velocity (37°/sec). Arrows in *D* and *E* indicate preferred direction of the same cell for motion of a long bar (*A*). Tuning is broader for the short than for the long bar, but preferred directions for the two stimuli are similar, and radically different from the preferred direction for noise. Note, however, the shift in preferred direction for the spot away from that for the bar, towards the major lobe of tuning for noise.

Nine noise-sensitive, symmetrically tuned cells were directionally biased or bidirectional for bar motion. In these cells, bar tuning was always symmetrical and comparably broad for opposite directions of motion, irrespective of whether noise evoked excitation when moving in only one (Fig. 6.2E, H) or in both directions (Figs. 6.3A-D, 6.5K-O) along a common axis. Suppression of spontaneous activity was seen on both sides of each excitatory profile for the bar, corresponding to opposite directions of motion.

(b) Asymmetrically Tuned Cells

Directional tuning for bar motion in noise-sensitive, asymmetrically tuned cells was characteristically broad (section 6.3, Table 6.2), and frequently lacked the suppression of firing on the sides of the excitatory profile (e.g. Figs. 6.1E, H, 6.7C) typical of noise sensitive cells with symmetrical bar tuning. Such suppression would have been apparent in most noise-sensitive, asymmetrically tuned cells, since they were predominantly Group 1 cells with high spontaneous activity. Occasionally, suppression was seen only on the sharper of the two flanks of tuning (Figs. 6.1F, J, 6.6F, J), or over a greater range of directions on this flank (Fig. 6.4A, E). In such cases, suppression was strongest at low velocities.

In noise-sensitive cells asymmetrically tuned for bar motion, tuning for noise could remain unimodal (Figs. 6.3E, H, 6.5F, J, 6.6F, J) or bimodal (Figs. 6.2A, D, 6.4F, J) throughout the range of velocities used, or alternatively, unimodal tuning could give way to bimodal tuning as velocity was increased (Figs. 6.1E, H, 6.4A, E). When tuning was unimodal, preferred directions for noise and bar motion were dissimilar, and bar tuning was broader on the flank closest to the preferred direction for noise. When noise tuning was bimodal, the two lobes were unequal in height or width, and bar tuning was broader on the flank closest to the major lobe of tuning for noise. Broadening of bar tuning on the flank closest to the preferred direction for noise has been previously reported for asymmetrically tuned area 17 complex cells with good noise sensitivity (Hammond, 1978a; Hammond

and Smith, 1983). The present results show that the relationship between the tuning profiles for bar and noise motion in asymmetrically tuned cells also obtains in area 18. Exceptionally asymmetrically tuned cells had a single preferred direction for noise at low velocity which was not obviously different from that for the bar. As velocity was increased, noise tuning became strongly bimodal with lobes of unequal strength. In such cases, the major lobe of tuning for noise at high velocity coincided with the broader flank of bar tuning (Fig. 6.4*A–E*).

In 10 noise-sensitive, asymmetrically tuned cells (3 in area 17, 7 in area 18) for which directional tuning comparisons had been made for motion of visual noise and a long bar over a range of velocities, tuning curves were also derived for moving noise and moving spot stimuli interleaved. In 6 cells (2 in area 17, 4 in area 18), tuning was compared, in addition, for noise and for a bar short with respect to minimum response field length. For the above comparisons, tuning curves were compiled using a velocity at which preferred directions for noise and a long bar were radically dissimilar. In Fig. 6.7*C–E*, which shows directional tuning comparisons for visual noise, for short and long bars, and for single spot stimuli in an area 18 cell lacking substantial length summation, tuning for noise was bimodal with lobes of unequal strength. The profile for both long and short bars was asymmetrical, with broader tuning on the flank closest to the major lobe of tuning for noise. Tuning was broader for the short than for the long bar, but the preferred directions for the two stimuli were similar, and radically different from the preferred direction for noise. Tuning for motion of the spot and the short bar was comparably broad, but the preferred direction for the spot shifted by 40° away from that for the bar, towards the major lobe of tuning for noise. The shift in preferred direction for spot stimuli obtained in all 10 noise-sensitive, asymmetrically tuned cells in which the appropriate tuning comparisons were made, including those which were unimodally tuned for noise at all velocities, and those showing substantial length summation.

Eight asymmetrically tuned cells were directionally biased or bidirectional for bar

motion. In 3 of these, bar tuning for motion in opposite directions along a common axis was comparably broad and asymmetrical, and modality of tuning for noise was consistent for opposite directions of motion (Fig. 6.1*E–H*). In 3 cells which were direction-selective for noise (Fig. 6.3*E–H*) bar tuning was narrower and more symmetrical for motion in the non-preferred than in the preferred direction. Exceptionally, bar tuning in the non-preferred direction was labile, the variations in width and profile being related to velocity-dependent changes in tuning for noise (Figs. 6.5*F–J*, 6.6*F–J*). Differences in width of tuning for opposite directions of bar motion were observed in both symmetrically (Fig. 6.5*A–E*) and asymmetrically (Figs. 6.2*A–D*, 6.4*A–E*, 6.5*F–J*) tuned noise-sensitive cells which were essentially direction-selective, but gave a negligible response to bar motion in the non-preferred direction. However, among cells directionally biased or bidirectional for bar motion, differences in bar tuning for opposite directions of motion were seen only in noise-sensitive, asymmetrically tuned cells; bidirectional or directionally biased cells, asymmetrically tuned for bar motion but noise-insensitive, all had comparably broad and asymmetrical tuning for opposite directions of bar motion.

(c) Labile Directional Tuning For Bar Motion

An unexpected feature of the present results was the high proportion of cells with directional tuning for bar motion which was labile and varied with velocity. Five cells showed a reversal in the direction of asymmetry in tuning for bar motion as velocity was increased (Fig. 6.6*K–O*). Seven cells had broader and more asymmetrical bar tuning at high than at low velocities (Fig. 6.6*A–E*); in 4 of these bar tuning was symmetrical at low velocity but markedly asymmetrical at higher velocities (Fig. 6.8*A–D*). Exceptionally (2 cells), the preferred direction for bar motion changed as velocity was increased (Fig. 6.8*E–I*). None of these variations in bar tuning could be ascribed to deepening of anæsthesia (Ikeda and Wright 1974) or to deterioration of the preparation. They seemed rather to be associated with velocity-dependent changes in directional tuning for noise.

Two examples of labile directional tuning for bar motion have already been illustrated in Fig. 6.6. In *A–E*, bar tuning was broader and more asymmetrical at high than at low velocities. With increase in velocity, tuning for noise became strongly bimodal with widely disparate peaks of unequal height. Bar tuning initially remained constant as velocity was increased but at the highest velocities used, there was an increase in the range of response directions on the flank to the right of the peak, which coincided with the major lobe of tuning for noise. The cell in *K–O* showed a reversal in the direction of asymmetry in tuning for bar motion, which was related to the velocity-dependent changes in the relative size of the two lobes in the bimodal tuning curve for noise.

Fig. 6.8 shows two examples of more radical changes in tuning for bar motion as a function of velocity. Bar tuning in the area 17 VBB cell in *A–D* was narrow and symmetrical at low velocity, with suppression of firing on both sides of the excitatory profile. Tuning became progressively broader and more asymmetrical with velocity, due to an increase in the range of response directions on the flank to the right of the peak. Over the same velocity range, there was a steep increase in the response to noise moving in directions corresponding to the broader flank of bar tuning. *E–I* shows an area 18 VHP cell with different preferred directions for bar motion at low and at high velocities. At low velocities (*E, F*), bar tuning was symmetrical and preferred directions for bar and noise motion were not obviously dissimilar. At a higher velocity (*G*), the tuning profile for the bar became asymmetrical with broader tuning on the flank closest to the preferred direction for noise, which was now radically different from that for the bar. At the highest velocities used (*H, I*), noise tuning was distinctly bimodal with lobes of unequal strength and the preferred direction for the bar shifted by 20° towards the major lobe of tuning for noise.

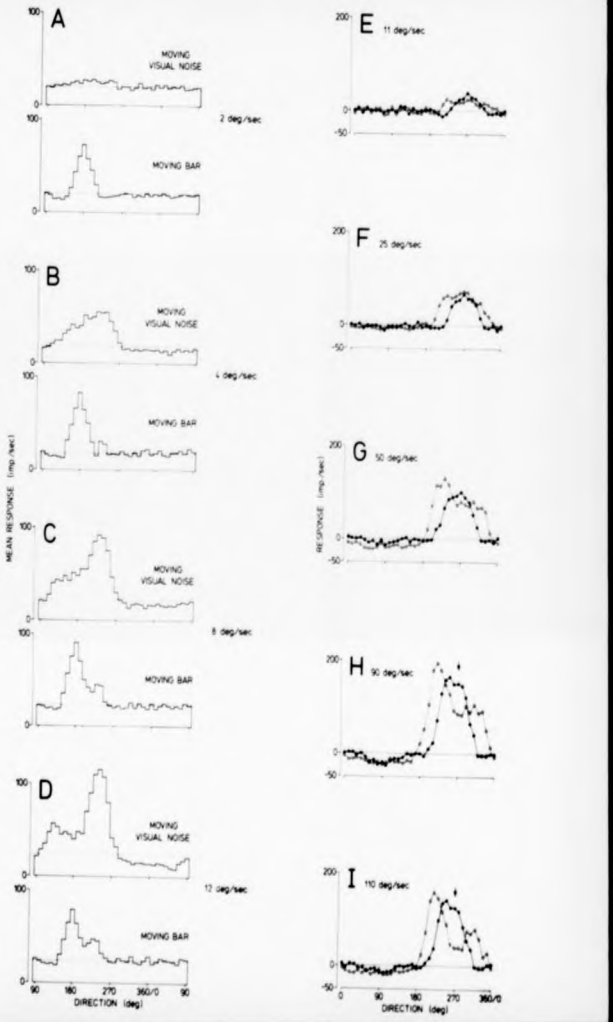
A
MOVING VISUAL NOISE
2 deg/sec
MOVING BAR
B
MOVING VISUAL NOISE
4 deg/sec
MOVING BAR
C
MOVING VISUAL NOISE
8 deg/sec
MOVING BAR
D
MOVING VISUAL NOISE
12 deg/sec
MOVING BAR
MEAN RESPONSE (imp/sec)
DIRECTION (deg)
E 11 deg/sec
F 25 deg/sec
G 50 deg/sec
H 90 deg/sec
I 110 deg/sec
RESPONSE (imp/sec)
DIRECTION (deg)

Fig. 6.8. Directional tuning comparisons for noise and bar motion over a range of velocities, in 2 Group 1 C-cells with labile tuning for bar motion. *A–D* an area 17 VBB cell with narrow, symmetrical bar tuning at low velocity but broad, asymmetrical tuning at high velocities. Conventions and derivation as in Fig. 6.1. Note that the progressive increase with velocity in width and asymmetry of tuning is associated with velocity-dependent changes in tuning for noise. *E–I* an area 18 VHP cell with different preferred directions for bar motion at low and high velocities. Conventions and derivation as in Fig. 6.4, except that arrows in *H* and *I* indicate preferred direction in the same cell for bar motion at lower velocities (*E–G*). Note that at high velocity, the peak in tuning for bar motion shifts towards the major lobe in the bimodal tuning curve for noise.

6.3. QUANTITATIVE COMPARISONS OF BROADNESS AND ASYMMETRY OF DIRECTIONAL TUNING FOR BAR MOTION IN AREA 17 AND AREA 18 CELLS

6.3.1. Quantitative Comparisons Of Broadness And Asymmetry Of Directional Tuning For Bar Motion In C-Cells, According To Noise Sensitivity And Bar Tuning Profile

Quantitative comparisons of broadness and asymmetry of directional tuning in C-cells according to noise sensitivity and bar tuning profile are shown in Table 6.2. Results from areas 17 and 18 were pooled since there were no significant inter-areal differences in broadness and asymmetry of tuning among any of the different cell classes in the Table. Values for directional tuning width, average half-width and ratio of half-widths in each cell were averages derived from tuning curves compiled at a number of velocities. Table values are means, with ranges and standard deviations in parentheses. Differences in broadness and asymmetry of tuning for bar motion at different velocities were trivial in symmetrically and asymmetrically tuned cells, but substantial in cells with labile bar tuning. Thus for cells of the latter type, the means of both the *average* and the *maximum* values for tuning width, average half-width and ratio of half-widths are shown in the Table; note that in many cases, smooth curves rather than straight lines were fitted to the data points (see section 6.2.), and thus the average half-width of tuning at half-height does not necessarily represent 25% of the total tuning width.

Of all C-cells, those with labile tuning for bar motion were the most broadly tuned. The difference in broadness of tuning for noise-sensitive cells with labile and asymmetrical bar tuning reached statistical significance (Mann-Whitney U-test: $P < 0.05$) when the *maximum* values for tuning width and average half-width in cells with labile bar tuning were considered. Among noise-sensitive C-cells, those with asymmetrical bar tuning were significantly more broadly tuned for direction than those with symmetrical tuning (Mann-Whitney U-test: $P < 0.001$). This

		DIRECTIONAL TUNING WIDTH (deg.)	AVERAGE HALF-WIDTH (deg.)	RATIO OF HALF-WIDTHS
NOISE-SENSITIVE				
LABILE (n = 14)	Max.	127.9 (60-180, 38.6)	34.6 (20.0-50.5, 8.4)	1.94 (1.20-2.80, 0.6)
	Mean	110.4 (68-180, 33.1)	30.5 (19.3-49.3, 7.8)	1.55 (1.11-2.08, 0.3)
ASYMMETRICAL (n = 18)		103.3 (60-180, 47.3)	27.1 (11.4-47.8, 10.3)	1.89 (1.30-2.75, 0.5)
SYMMETRICAL (n = 12)		53.5 (30-80, 15.4)	14.5 (9.1-21.1, 3.8)	≤ 1.20
NOISE-INSENSITIVE				
ASYMMETRICAL (n = 11)		72.3 (60-130, 20.7)	19.1 (15.1-32.6, 4.7)	1.56 (1.25-1.90, 0.2)
SYMMETRICAL (n = 5)		66.0 (30-100, 30.5)	17.2 (9.0-24.2, 6.7)	≤ 1.20

Table 6.2. Quantitative comparisons of broadness and asymmetry of directional tuning for bar motion in end-free C-cells, according to noise sensitivity and bar tuning profile (data from areas 17 and 18 pooled). Directional tuning width: total range of response directions for bar motion. Average half-width: average of half-widths of directional tuning at half-height after fitting curves by eye to data points (see text for details of procedure). Ratio of half-widths: ratio of half-widths of tuning at half-height taking the greater half-width as numerator in each case. Values for each cell were averages derived from directional tuning curves compiled at a number of velocities. Table values are means, with ranges and standard deviations in parentheses. In addition, the means of the *maximum* values for directional tuning width, average half-width and ratios of half-width are shown separately for 'labile' cells, since their bar tuning varied dramatically with velocity. Two end-free asymmetrically tuned C-cells whose tuning profile for bar motion was symmetrical in terms of half-width at half-height, but had a drawn-out tail on one flank are excluded from comparisons of ratios of half-width.

difference could not be attributed to the relatively high proportion of asymmetrically tuned C-cells in Group I: symmetrically tuned cells had the narrowest bar tuning among C-cells in Group I (mean width: 56.7°, mean average half-width: 15.4°) and Group II (mean width: 56.0°, mean average half-width: 13.6°). Of all C-cells, those symmetrically tuned and sensitive to noise had the narrowest bar tuning. The difference in broadness of tuning between noise-sensitive and noise-insensitive C-cells with symmetrical bar tuning did not reach statistical significance, but asymmetrically tuned cells insensitive to noise were significantly more broadly tuned for direction than noise-sensitive, symmetrically tuned cells (Mann-Whitney U test, width: $P < 0.05$, average half-width: $P < 0.025$). This difference is remarkable when one considers the substantially broader tuning of noise-sensitive (particularly Group I) C-cells compared with their noise-insensitive counterparts (see Chapter 5). Among noise-insensitive C-cells, there were no significant differences in broadness of directional tuning between those symmetrically and those asymmetrically tuned for bar motion, or between those in groups III and IV. Among asymmetrically tuned C-cells, those sensitive to noise were significantly more broadly and more asymmetrically tuned than those insensitive to noise (Mann-Whitney U test, $P < 0.025$). The ratios of half-widths of noise-sensitive, asymmetrically tuned cells were not substantially different from the maximum values for cells with labile bar tuning.

6.3.2. Quantitative Comparisons Of Broadness And Asymmetry Of Directional Tuning For Bar Motion In C-, B-, S- And A-Cells In Areas 17 And 18

The only previous quantitative study of directional tuning of area 18 cells is that of Hammond and Andrews (1978), whose cell classification procedure was radically different from the one used here. The present study thus provides the first quantitative comparisons of directional tuning of C-, B-, S- and A-cells in area 18. Means of directional tuning widths and of average half-widths of area 18 cells in

CELL CLASS		DIRECTIONAL TUNING WIDTH (deg.)	AVERAGE HALF-WIDTH (deg.)
C	A17 (n = 28)	83.2 (30 - 180; 39.7)	22.6 (9.0 - 47.4; 10.4)
	A18 (n = 32)	96.4 (40 - 180; 46.3)	25.5 (10.0 - 50.5; 10.5)
S	A17 (n = 7)	40.0 (20 - 60; 14.1)	12.4 (7.0 - 19.1; 3.9)
	A18 (n = 13)	57.3 (40 - 90; 14.5)	17.4 (9.3 - 26.7; 4.4)
B	A17 (n = 5)	46.0 (20 - 80; 24.1)	13.9 (7.5 - 22.0; 5.8)
	A18 (n = 10)	68.0 (20 - 100; 28.2)	18.6 (9.5 - 25.3; 5.6)
A	A18 (n = 4)	75.0 (70 - 80; 5.5)	23.5 (17.0 - 28.0; 4.9)

Table 6.3. Quantitative comparisons of broadness of directional tuning for bar motion of C-, S, B- and A-cells in areas 17 and 18. The single A-cell recorded in area 17 is not included in the Table. Directional tuning width: total range of response directions for bar motion. Average half-width: average of half-widths of tuning at half-height after fitting curves by eye to data points (see text for details of procedure). Values are means, with ranges and standard deviations in parentheses. Note that the *maximum* values for directional tuning width and average half-width in cells with labile bar tuning were used in calculating the mean values for C-cells.

different classes are shown in Table 6.3, together with values for area 17 cells for comparison. The important comparisons in the Table are between area 18 cells in different classes and between C-cells in areas 17 and 18. The number of S- and B-cells recorded in area 17 was small, and they are included in the Table largely for completeness. The means for C-cells in areas 17 and 18 were calculated using the *maximum* tuning widths and *maximum* average half-widths of cells with labile bar tuning. The use of mean rather than maximum values for cells with labile bar tuning did not, however, substantially alter the assessment of broadness of tuning of C-cells either in area 17 (mean width 80·2°, mean average half-width 22·0°) or in area 18 (mean width 91·4°, mean average half-width 24·3°). In both areas, C-cells had the broadest, S-cells the narrowest tuning for bar motion. The values for broadness of tuning in the small sample of area 17 S-cells are in line with those of others for simple or S-cells (Henry et al., 1973; Watkins and Berkley, 1974; Hammond and Andrews, 1978; Heggelund and Albus, 1978; Kato et al., 1978; Leventhal and Hirsch, 1978; Orban, 1984). C-cells were significantly more broadly tuned than S-cells, both in area 17 (width $z = 5.18$, $P = 0.0010$; average half-width $z = 2.39$, $P = 0.0057$) and in area 18 (width $z = 2.46$, $P = 0.0007$; average half-width $z = 2.74$, $P = 0.0084$). S-cells in area 18 were, however, significantly more broadly tuned than their counterparts in area 17 (Mann-Whitney U test, $P < 0.025$). C-cells in areas 17 and 18 did not differ significantly in broadness of directional tuning. In area 18, C-cells were significantly more broadly tuned than B-cells (width $z = 1.65$, $P = 0.0495$; average half-width $z = 1.96$, $P = 0.0275$), and A-cells were significantly more broadly tuned than S-cells (Mann-Whitney U test, width $P < 0.025$; average half-width $P < 0.05$).

There were no inter-areal differences in the ratios of half-widths of S- and B-cells, and no statistically significant differences between the values for S- (1·17), B- (1·21) and A-cells (1·31) from areas 17 and 18. S-, B- and A-cells with asymmetrical bar tuning had almost identical ratios of half-widths. The ratios of half-widths for the combined sample of S-, B- and A-cells with asymmetrical bar tun-

ing (1·41) did not differ significantly from those of asymmetrically tuned C-cells insensitive to noise, but were significantly smaller than those of noise-sensitive, asymmetrically tuned C-cells (Mann-Whitney U test; $P < 0{\cdot}025$).

CHAPTER 7

THE MODULATORY INFLUENCE OF MOVING VISUAL NOISE BACKGROUNDS ON RESPONSES OF CELLS IN AREA 18 TO MOVING ORIENTED STIMULI

7.1: Modulatory Influence Of A Moving Noise Background On Bar-Evoked Responses As A Function Of Bar Length

7.2: Modulatory Influence Of A Moving Noise Background On Bar-Evoked Responses As A Function Of Stimulus Velocity

The present chapter describes results on the modulatory influence of a moving textured background of pseudo-random, static visual noise on the responses of cells in area 18 to moving oriented foreground stimuli. Comparisons were made, virtually simultaneously, between the response to an optimally-oriented bar swept in both directions along the axis orthogonal to its orientation, alternately in synchrony with its noise background, in the same direction and with the same phase, velocity and amplitude of motion (combination stimulus), and independently across the same *stationary* noise background. Bar width was set optimally for each cell, but bar length and stimulus velocity were systematically varied. The modulatory influence of moving noise backgrounds on moving bar responses was investigated primarily in noise-insensitive cells (members of groups III and IV), classified on the basis of their lack of response to noise motion alone (see Chapter 5), though comparable measurements were made on a few noise-sensitive cells. Incidental observations on the influence of bar length on velocity-response functions of area 18 cells are also reported.

7.1. MODULATORY INFLUENCE OF A MOVING NOISE BACKGROUND ON BAR-EVOKED RESPONSES AS A FUNCTION OF BAR LENGTH

In all 37 noise-insensitive cells in area 18, the influence of synchronously moving noise backgrounds was investigated on responses to optimally-oriented bar stimuli of fixed width but variable length moving at the preferred velocity. The bar was systematically increased in length while maintaining its symmetry about the centre of the receptive field, the locus of maximum response along the receptive field axis being determined by the minimum response field method. The order of testing with bars of different length was randomized. The shortest comparison bar used was that which evoked a consistent response, a bar which was too short elicited weak and variable drive, providing a poor criterion for comparison

with the combination stimulus. The longest bar that could be generated was 20° in length. The experimental procedure was designed to explore the modulatory influence of moving noise backgrounds on bar-evoked responses as a function of bar length, and additionally allowed the presence or absence and magnitude of response modulation to be related to the conventional length-response characteristics of each cell. The results could be compared directly with those of previous investigations of the modulatory influence of synchronous background motion on the bar-evoked responses of area 17 cells (Hammond and MacKay 1977, 1981b; Hammond and Smith 1984), in which the parameters of the foreground bar were set optimally for each cell, and related to those of comparable studies in area 17 (Hoffmann and von Seelen 1978; Hoffmann et al. 1980) and area 18 (Dinse and von Seelen 1981b), in which a field of Gaussian noise was superimposed on a moving bar in order to simulate a signal detection task. Results for end-free and end-stopped cells are described separately.

7.1.1. End-Free Cells

Thirty-one of the 37 noise-insensitive cells in area 18 lacked significant end-inhibition (see Chapter 5 for classification of end-stopped cells). These comprised 11 S-cells, 11 C-cells, 6 B-cells and 3 A-cells. Results for cells in different classes are described together, since response modulation by moving noise backgrounds revealed no striking class-specific differences.

(a) Preferred Direction

In all end-free cells, the modulatory influence of moving noise backgrounds on responses to bar motion in the preferred direction was critically dependent on the length of the bar used to obtain a criterion response. As can be seen in Fig. 7.1, background motion exerted marked suppression of response to a short bar, but its effectiveness declined progressively as the comparison bar was increased in

length. Fig. 7.1A shows for a C-cell with restricted length summation, representative PSTHs in response to a bar of variable length moving alternately in unison with a background of visual noise and independently across the same stationary noise background. Responses of this cell were chosen for illustration for two reasons. First, stimulation with a short bar yielded a good criterion response against which the powerful suppressive influence of the moving noise background could be observed. Second, the progressive relief from the suppressive influence of synchronous background motion as the comparison bar was increased in length is clearly evident from a comparison of PSTHs, since the criterion response remained relatively constant, while response to the combination stimulus increased progressively with bar length over a wide range. These trends are seen more clearly in Fig. 7.1*B*, which presents graphically results from the cell in *A*, but for a greater number and wider range of bar lengths. Results are illustrated for motion in the preferred direction only. Length summation was restricted for the bar (filled circles), but substantial for the combination stimulus (open circles). Percent suppression (triangles) was maximal for the shortest bar used and declined progressively with increasing bar length, but over a range more extensive than the length of the minimum response field (indicated by arrow), which in turn significantly exceeded the limit value of length summation.

The improvement in the relative response to the combination stimulus as bar length was increased was presumably due to the progressive relief from the suppressive influence of moving noise as the bar obliterated an increasing amount of the noise background along the longitudinal axis of the receptive field. In this respect the result was unremarkable. Three aspects are, however, worth emphasizing. First, the decline in percent suppression was non-linear, becoming progressively flatter in slope as bar length was increased, until an asymptotic value was reached. Second, the range over which percent suppression declined with bar length suggests that the suppressive influence of textural elements was detectable outside the mapped receptive field along its axis. Finally, conventional stimulation with a long bar showed this cell to be rather indifferent to synchronously moving

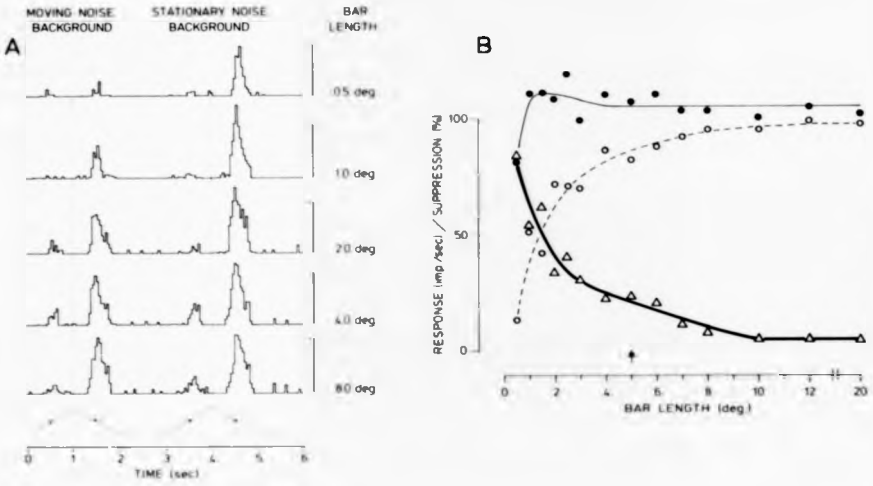
A
MOVING NOISE BACKGROUND
STATIONARY NOISE BACKGROUND
BAR LENGTH
0.5 deg
1.0 deg
2.0 deg
4.0 deg
8.0 deg
0
1
2
3
4
5
6
TIME (sec)
B
RESPONSE (imp/sec) / SUPPRESSION (%)
100
50
0
0
2
4
6
8
10
12
20
BAR LENGTH (deg.)

Fig. 7.1. Modulatory influence of synchronous motion of a background of static visual noise on responses to a moving bar of variable length, in an end-free C-cell with restricted length summation. *A* Representative PSTHs demonstrating the progressive relief from suppressive influences of the moving noise background as the comparison bar is systematically increased in length, while maintaining its symmetry about the centre of the minimum response field. Each PSTH compares the response to an optimally-oriented bar of given length and fixed width (0·7°) moving at 7°/sec in both directions along the axis orthogonal to its orientation, alternately in synchrony with its noise background, with the same phase, velocity and amplitude (7°) of motion, and independently across the same stationary noise background. The trace beneath the PSTHs indicates the duration of stimulus motion, and of inter-sweep intervals during which only the stationary noise background was present, to yield a measure of resting discharge level. Each PSTH was compiled from 16 consecutive 6sec cycles. Bin-width 40ms. Vertical scales indicate 100 imp/sec throughout. *B* Graphical representation of results from the cell in *A* for the preferred direction of motion only. Filled circles: response to a bar moving across a stationary noise background. Open circles: response to the bar moving in unison with the same noise background (combination stimulus). Thin, solid and broken lines are the by-eye fits to the filled and open circles respectively. Response was derived from PSTHs (16 presentations) and expressed as peak firing frequency (averaged over the 3 adjacent bins containing the highest spike count), subtracted from mean spontaneous activity assessed at the time each PSTH was compiled. Arrow indicates length of minimum response field. Note that length summation is restricted for the bar, but substantial for the combination stimulus, extending beyond the limits of the minimum response field. Triangles indicate percent suppression of the response to a moving bar of fixed length by synchronous motion of the noise background. Thick, solid line is the by-eye fit to the data points. Note that percent suppression greatest for the shortest comparison bar used, declines non-linearly with increasing bar length, over a range more extensive than the length of the minimum response field.

noise backgrounds, yet a reduction in bar length revealed a powerful suppressive influence of background motion on cell responsiveness. Indeed, maximum response suppression in this cell (83%) was greater than in any other cell recorded.

It is worth emphasizing that the results from cells with restricted length summation differed from those obtained in other end-free cells in two important respects. First, in cells with restricted length summation, it was possible to demonstrate that the magnitude of suppression exerted by background motion was related not to the strength of the criterion response (which remained relatively constant), but to the length of the bar used to obtain a criterion response. In cells with substantial length summation, the situation is of course more complicated since lengthening the bar elicits an increase in excitation in addition to providing greater coverage of the noise background. Second, in cells with restricted length summation, not only percent suppression but also response reduction declined nonlinearly with bar length. The significance of this observation will be taken up in Discussion.

The magnitude of response modulation exerted by moving noise backgrounds was similarly related to the length of the comparison bar in end-free cells showing substantial length summation. Fig. 7.2 shows length-response curves in a B- (*A* and *B*), C- (*C* and *D*) and S-cell (*E* and *F*) for interleaved presentation of a bar and the combination stimulus moving in preferred and opposite directions (upper and lower functions respectively), together with the ratio of the response to a moving bar of fixed length with the noise background alternately moving and stationary. In these and all ensuing comparisons, response ratio is plotted in preference to percent suppression since when long bars were used, response to the combination stimulus could exceed, though not significantly (see later), that to the bar alone. The suppressive influence of moving noise backgrounds on responses to bar motion in the preferred direction was strongest when the comparison bar was short. Response to both the bar and the combination stimulus increased with bar length, but percentage increase was greater for the combination stimulus presumably be-

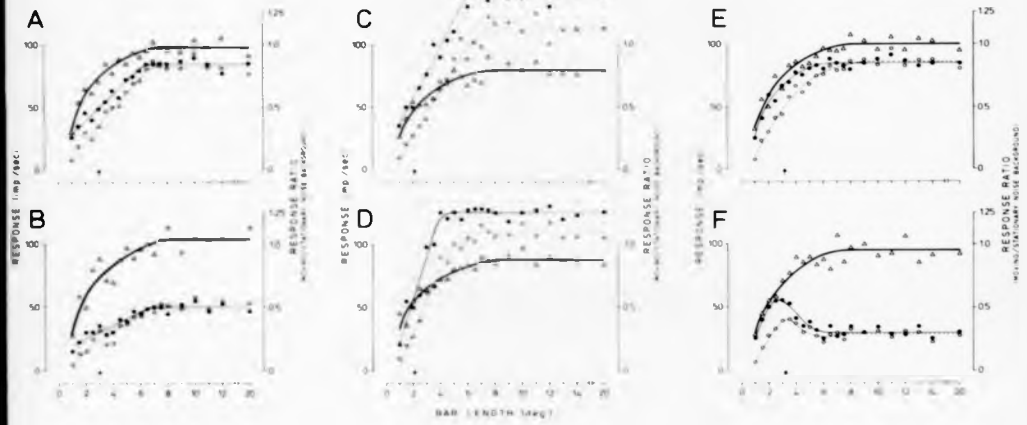
A
B
C
D
E
F
RESPONSE (imp/sec)
RESPONSE RATIO
BAR LENGTH (deg)

Fig. 7.2. Comparison in 3 length-summating, end-free cells ($A+B$, $C+D$, $E+F$) of responses to an optimally-oriented bar of fixed width but variable length, moving at the optimal velocity in preferred and opposite directions (upper and lower functions respectively) with its noise background either held stationary or swept synchronously in the same direction with the same phase, velocity and amplitude of motion. Derivation and conventions as in Fig. 7.1, except that triangles represent the ratio of the response (right vertical scale) to a moving bar of fixed length with the noise background alternately moving and stationary. $A+B$, B-cell; minimum response field width 1·7°, bar width 0·7°, stimulus excursion 5°, velocity 23°/sec. $C+D$, C-cell; minimum response field width 3·7°, bar width 1·0°, stimulus excursion 10°, velocity 82°/sec. $E+F$, S-cell; minimum response field width 1·5°, bar width 0·7°, stimulus excursion 5°, velocity 23°/sec. Note that in all cells, the function relating response ratio and bar length is comparable for preferred and opposite directions of motion, irrespective of whether the extent of length summation in the two directions is similar ($A+B$), slightly ($C+D$) or radically different ($E+F$); the relative response to the combination stimulus increases non-linearly with bar length, over a range which either matches (A, B, C) or exceeds (D, E, F) the zone of length summation, until an asymptotic value is reached at which the moving noise background is either suppressive of bar response ($C+D$) or has a negligible modulatory influence ($A+B$, $E+F$). Note that there is no fixed relationship from cell to cell between the slopes of length summation for the bar and the combination stimulus.

cause, as it was lengthened, the bar obliterated an increasing amount of the noise background, providing progressive relief from the suppressive influence of moving noise, in addition to causing an increase in excitation. As in end-free cells with restricted length summation, the increase in the relative response to the combination stimulus was non-linear, becoming progressively flatter in slope as the bar was increased in length, until an asymptotic value was reached.

In general, the maximum amount of suppression observed in each cell was related to the minimum length of the comparison bar against which reliable measurements were possible. In the cells illustrated in Fig. 7.2, a short bar moving in the preferred direction evoked a consistent response, which was powerfully suppressed by synchronous background motion. However, a few cells had their responses to bars of similar length less substantially suppressed, suggesting that they received a less potent noise-sensitive inhibitory input. In many cells requiring appreciable length summation for effective drive, longer starting lengths for the comparison bar resulted in less potent suppressive effects and less marked non-linearity of the curve relating response ratio and bar length. Nevertheless, the overall trends were consistent with those illustrated.

The relative response to the combination stimulus reached a plateau only when bar length matched (Fig. 7.2*A*) or exceeded (Fig. 7.2*D, E*) the extent of length summation for the bar alone. In the latter case, the rising phase for the combination stimulus became flatter in slope as bar length was increased beyond the limit value of length summation for the bar, presumably because the improvement in the response to the combination stimulus was now due solely to obliteration of the background by the moving bar, which itself provided no further increase in excitation. This would imply that texture elements lying beyond the height of the receptive field were capable of modulating responsiveness. However, it was difficult to determine precisely the lengthwise extent of background influence, because when the modulatory influence of background motion was insubstantial, the data points representing the relative response to the combination stimulus showed con-

siderable scatter. Moreover, for a bar of fixed length, the influence of background motion showed a high degree of sweep-to-sweep variability. It was clear, however, that no cell showed the significant enhancement of response to long bars observed by Hammond and MacKay (1981b) in some area 17 simple cells.

Comparable measurements were made on 4 noise-sensitive, Group I C-cells in area 18. Even in cells with restricted length summation, synchronous motion of the noise background *enhanced* the peak response to a short bar. Response enhancement declined with increase in the length of the comparison bar, but over a range more restricted than the corresponding decline in percent suppression in noise-insensitive cells. The influence of background motion on the response to a long bar was weak or negligible, and much less than predictable from an additive combination of the separate responses to bar and noise motion alone. Typically, reducing the length of the comparison bar produced no increase in response modulation until bar length was significantly less than half the length of the receptive field. Thereafter, response enhancement increased dramatically. Maximum response enhancement was observed when, in the limit, length reduction made the bar effectively a spot. In the 2 cells with substantial length summation, the response to moving noise was so large as to effectively mask the weak response to a short bar.

(b) Non-Preferred Direction

It was of interest to compare the modulatory influence of moving noise backgrounds on responses to bar motion in the preferred and opposite directions as a function of bar length, particularly since in some cells length-response functions were found to differ for the two directions of motion. Moreover, it was hoped that a comparison of the magnitude of suppressive influences on responses to bar motion in the preferred and non-preferred directions would provide insight into the properties of the noise-sensitive suppressive input. Background motion might conceivably suppress by a constant amount or by a constant percentage the response to a bar of fixed length moving in preferred and opposite directions. Alternatively, the magnitude of suppression in the two directions might be independent.

Eight cells were completely direction-selective and had zero spontaneous activity. In these cells, observations were thus limited to the preferred direction. Fifteen of the 31 end-free noise-insensitive cells gave a response to bar motion in the

non-preferred direction which was sufficient to yield a reliable length-response curve. These were divided into three categories by comparing length-response functions for motion in the preferred and non-preferred directions. In 7 cells (Fig. 7.2*A* and *B*), length-response functions were comparable for preferred and opposite directions of motion, both with respect to optimal bar length and the absence of end-inhibition (cf. Orban et al. 1979a; Hammond and MacKay, 1983b, 1985; Hammond and Ahmed, 1985) while in 2 cells, the limit value of length summation differed significantly for the two directions of motion (Fig. 7.2*C* and *D*). The remaining 6 cells showed substantial length summation in the preferred direction, but restricted length summation and end-zone inhibition in the non-preferred direction (Fig. 7.2*E* and *F*). Orban et al. (1979a,b), who reported the existence of such cells in area 17, concluded that the inhibition in the non-preferred direction reflects the length summation requirements of the inhibitory mechanism responsible for the direction selectivity of the discharge region, rather than being due to the presence of direction-selective inhibitory end-zones. Note that the cell in Fig. 7.2*E* and *F* showed strong directional bias when stimulated with a bar of optimal length for the preferred direction, but responded bidirectionally when bar length was optimal for motion in the non-preferred direction. Hammond and Mouat (1986) have recently reported changes in directional bias as a function of stimulus length in area 17 complex cells.

Of the 15 cells in which length-response functions were prepared for both the preferred and opposite directions of motion, 7 showed strong directional bias. The dilemma in these cells was that, on the one hand, responses to bars of suboptimal length moving in the non-preferred direction were weak and variable, providing a poor criterion for comparison with the combination stimulus, while on the other, the modulatory influence of background motion on the response to bars of near optimal length was insubstantial. Thus, the data points representing the relative response to the combination stimulus as function of bar length showed considerable scatter.

In 8 cells, however, the response in the non-preferred direction was sufficient to allow quantitative comparisons with the response to the combination stimulus, as a function of bar length. Fig. 7.2 shows results for 3 end-free cells, each representative of one of the three categories defined above according to length-response functions for preferred and opposite directions of motion. Notwithstanding in direction-biased cells, the greater degree of scatter of data points for the non-preferred compared with the preferred direction (*A* and *B*, *E* and *F*), the relative response to the combination stimulus increased with bar length over a comparable range for the two directions of motion. In Fig. 7.2*A* and *B*, the increase with bar length in the relative response to the combination stimulus matched the extent of length summation, which was comparable for preferred and non-preferred directions. In Fig. 7.2*C* and *D*, length summation was more extensive in the preferred than in the non-preferred direction. In the non-preferred direction, the increase in the relative response to the combination stimulus was significantly more protracted than the extent of length summation. Fig. 7.2*E* and *F* shows an S-cell with characteristically substantial length summation in the preferred direction, but restricted length summation and apparent end-inhibition in the non-preferred direction. In the preferred direction, the relative response to the combination stimulus increased with bar length over a range marginally more extensive than the zone of length summation while, in the non-preferred direction, the increase in relative response was considerably more protracted than the length summation profile.

For a bar of fixed length, the relative response to the combination stimulus, and hence percent suppression, was of comparable magnitude for preferred and opposite directions of motion. Thus in cells with significant directional bias (Fig. 7.2*A* and *B*), the *reduction* in the response to a bar of suboptimal length by synchronous motion of the noise background was greater in the preferred than in the non-preferred direction. Of 16 end-free cells classified as direction-selective, 8 gave a weak response to bar motion in the non-preferred direction when some bar lengths were used. Seven of these, and all the cells with strong directional bias

mentioned above, gave a response to the combination stimulus in the non-preferred direction even when a response reduction by background motion comparable to that observed in the preferred direction would have been sufficient to abolish the response in the non-preferred direction. These observations would seem to exclude the possibility that synchronous motion of the noise background reduced by a fixed amount the response to bar motion in the preferred and opposite directions.

In only 1 cell was percent suppression greater in the non-preferred than in the preferred direction. When some bar lengths and stimulus velocities were used, the cell responded weakly to bar motion in the non-preferred direction, but was direction-selective for the combination stimulus. Interestingly, in this cell, synchronous motion of the bar and its noise background in the non-preferred direction was capable of suppressing spontaneous activity, but only when motion of the bar alone evoked a response. When motion of the bar elicited weak excitation, synchronous motion of the noise background abolished the evoked response and suppressed spontaneous activity. When motion of the bar caused suppression of spontaneous activity, null-suppression was stronger for the combination stimulus. This is comparable to the situation observed in all cells for motion in the preferred direction, whereby the noise background had little or no influence on cell activity when moving alone, but could cause powerful response suppression when moved in synchrony with the bar. The suppression of spontaneous activity by synchronous motion of the bar and its noise background, though seen in only one cell, suggests that moving noise is capable of providing a post-synaptic inhibitory input.

7.1.2. End-Stopped Cells

The results reported here, together with those from previous studies, suggest strongly that the suppressive influence exerted by moving noise backgrounds is distinct from end-zone inhibition. Thus, Hammond and MacKay (1981b) reported that in the same *end-free* simple cells in area 17, whole-field background texture motion was suppressive of bar response, while a patch of moving texture

located outside the receptive field along its axis caused response facilitation. The present study has demonstrated in area 18 powerful suppressive influences of moving noise backgrounds in end-free cells of all classes by systematically varying the length of the comparison bar. Hammond and Smith (1984), on the other hand, while attributing the suppressive influence of moving noise backgrounds on the responses of some area 17 complex cells to the presence of end-inhibition, reported one end-stopped example whose bar responses were uninfluenced by synchronous background motion. It was thus of interest to determine in each end-stopped cell the modulatory influence of background motion on responses to bars of variable length, for comparison with the length of the inhibitory end-zones and the magnitude of end-zone inhibition.

(a) Preferred Direction

Only 6 noise-insensitive cells in area 18 were classified as end-stopped. These comprised 4 S_H-cells, 2 C_H-cells and 1 A_H-cell. With minor variations, results were uniform from cell to cell, in that the relative response to the combination stimulus increased non-linearly with bar length, they were consistent with those presented for end-free cells. Fig. 7.3 shows length-response curves in a C_H- (*A* and *B*) and an S_H-cell (*C* and *D*) for motion of a bar and the combination stimulus in preferred and non-preferred directions (upper and lower functions respectively), together with the ratio of response to a bar of fixed length with the noise background alternately moving and stationary. In the preferred direction, length summation was much more restricted than the length of the minimum response field (mapped with a short oscillating bar), indicative of an overlap between discharge region excitation and end-inhibition. Such an overlap of excitation and inhibition has previously been demonstrated in end-stopped cells in area 17 (Sillito, 1977; Henry et al., 1978a; Orban et al., 1979b). The relative response to the combination stimulus increased with bar length over a range which was considerably more extensive than the length summation zone, matched or exceeded the length of the minimum response field and was unrelated to the length

A
B
C
D
RESPONSE (imp/sec)
RESPONSE RATIO
BAR LENGTH (deg)
0
50
100
0.5
1.0
1.25
2
4
6
8
10
12
14
16
18
20

Fig. 7.3. Comparison of responses in a C_H- ($A+B$) and an S_H-cell ($C+D$) to an optimally-oriented bar of fixed width but variable length moving at the optimal velocity in preferred and opposite directions (upper and lower functions respectively), with its noise background either held stationary or swept synchronously in the same direction with the same phase, velocity and amplitude of motion (combination stimulus). Derivation and conventions as in Fig. 7.2. $A+B$: minimum response field width: 4.2°; bar width: 1°; stimulus excursion: 10°; velocity: 31°/sec. $C+D$: minimum response field width: 2.3°; bar width: 0.8°; stimulus excursion: 9°; velocity: 9°/sec. Note that the relative response to the combination stimulus increases non-linearly with bar length over a comparable range for preferred and opposite directions of motion. In $A+B$, the increase is more protracted than the length summation profile, but relative response reaches a plateau within the confines of the inhibitory end-zones. In C, the response to the combination stimulus increases with bar length over a range more extensive than either the zone of length summation or the length of the end-zone inhibitory region. Note, in particular, that end-zone inhibition is absent in the non-preferred direction (D), whereas background motion is suppressive of bar response in both preferred and non-preferred directions.

of the inhibitory end-zones. One rider to this is that in cells with powerful end-zone inhibition (Fig. 7.3*A*), stimulation with long comparison bars yielded weak criterion responses, and thus the data points representing relative response to the combination stimulus showed considerable scatter. Note that in Fig. 7.3*A*, background motion had a negligible modulatory influence on the response to an 8°-long comparison bar, while extending the same bar in length caused an increase in end-zone inhibition. Conversely in Fig. 7.3*C*, increasing bar length beyond 3.5° caused no further increase in end-zone inhibition, but provided progressive relief from the suppressive influence of background motion. There was no fixed relationship between the magnitude of end-zone inhibition and of suppression caused by synchronous background motion. Thus in Fig. 7.3*A*, percent suppression of the response to a bar of optimal length by the moving noise background (around 35%) was not as strong as percent end-inhibition (around 80%), while in Fig. 7.3*C*, end-inhibition and the suppressive influence of the moving noise background were of comparable strength.

(b) Non-Preferred Direction

In 3 of the 6 end-stopped cells, response to bar motion in the non-preferred direction provided a satisfactory criterion for comparison with the response to the combination stimulus. As in end-free cells, the relative response to the combination stimulus increased with bar length over a comparable range for preferred and opposite directions. In 2 cells, optimal stimulus length, the extent of the end-zone inhibitory region and percent end-inhibition were comparable for the preferred and opposite directions (Fig. 7.3*A* and *B*). In the most interesting end-stopped cell, the inhibitory end-zones were direction selective (Fig. 7.3*C* and *D*), as has been reported for a minority of end-stopped cells in area 17 (Orban et al. 1979*b*), whereas the moving noise background suppressed responses to bar motion in both preferred and non-preferred directions. The results from this cell provide further evidence for the independence of end-zone inhibition and response suppression caused by synchronous background motion.

7.1.3. Quantitative Comparisons Of The Suppressive Influence Of Moving Noise Backgrounds On The Responses To Bars Of Optimal And Suboptimal Length

Table 7.1 shows quantitative comparisons of the suppressive influence of moving noise backgrounds on responses to bars of optimal and suboptimal length, according to cell class. Table layout and derivation are explained in the Table legend. Comparisons are for the preferred direction of motion only, using a bar of optimal width moving at the preferred velocity. Thus, results for bars of optimal length can be compared directly with those from previous studies in which stimulus parameters were set optimally for each cell. While end-stopped cells had a clearly-defined optimal bar length, end-free cells cells gave a response of relatively constant magnitude once length summation had been attained. A 20°-long bar was arbitrarily taken as the optimum for all end-free cells, since they are conventionally stimulated with long bars. The proportion of cells in which responses to bars of optimal length were *significantly* suppressed (> 10%) by moving noise backgrounds, together with mean percent suppression, was greater in end-stopped than in end-free cells. There were no significant differences in the values for end-free cells in different classes. Mean percent suppression of response to bars of optimal length for all end-free cells, including those showing *insignificant* response suppression, was as low as 14%. These results, rather than indicating a difference between end-free and end-stopped cells in susceptibility to the suppressive influence of moving noise backgrounds, reflect the finding that percent suppression was greater for short than for long bars in all cells, regardless of their length-summation characteristics. Thus for bars of optimal length (as defined here), response suppression would be expected *a priori* to be higher in end-stopped cells by virtue of their preference for shorter bars.

All cells had their responses to bars of suboptimal length markedly suppressed, though not abolished, by synchronous motion of the noise background. Percent suppression was invariably higher for bars of suboptimal length than for optimal

NOISE BACKGROUND SUPPRESSION (>10%)

CELL CLASS	OPTIMAL BAR LENGTH (20° except H-cells)		SUBOPTIMAL BAR LENGTH	
	PERCENTAGE OF CELLS	PERCENT SUPPRESSION	PERCENTAGE OF CELLS	PERCENT SUPPRESSION
S (n=11)	55	25 (14-35)	100	43 (27-68)
C (n=11)	55	21 (12-31)	100	59 (29-78)
B (n=6)	50	25 (18-29)	100	62 (36-83)
A (n=3)	67	24 (20-28)	100	62 (39-65)
TOTAL (n=31)	55	23 (12-35)	100	53 (27-83)
H (n=6)	100	45 (33-55)	100	71 (60-80)

Table 7.1. Quantitative comparisons of the suppressive influence of moving noise backgrounds on responses to bars of optimal and suboptimal length in noise-insensitive cells (members of groups III and IV) of different classes (S, C, B, A). H indicates end-stopped cells of all classes. Note that a bar length of 20° was arbitrarily chosen as the optimum for all end-free cells. Suboptimal bar length refers to the shortest bar which, when presented against a stationary noise background, was capable of evoking a consistent response. Results are for motion in the preferred direction only, with bar width and stimulus velocity set optimally for each cell. The values for percent suppression were derived from the by-eye fits to the data points representing the ratio of the response to the bar with the noise background alternately moving and stationary. The percentage of cells showing significant suppression (> 10%) of responses to bars of either optimal or suboptimal length by motion of the noise background is indicated for each class and for the total number of end-free cells. Mean percent suppression is shown for the same cells, with ranges in parentheses. Note that the proportion of cells whose responses to bars of optimal length were significantly suppressed by synchronously-moving noise backgrounds, together with percent suppression, was greater in end-stopped than in end-free cells. In all cells, background motion suppressed, but did not abolish, responses to bars of suboptimal length. Percent suppression was higher for suboptimal than for optimal length bars. Mean percent suppression of response to suboptimal length bars was, however, greater in end-stopped than in end-free cells.

length bars. In general, maximum suppression was related to the minimum length of the comparison bar against which reliable measurements were possible, and was thus higher in end-stopped than in end-free cells: a very short bar provided potent drive to all end-stopped cells, whereas many end-free cells required appreciable length summation for response threshold to be exceeded. By the same token, S-cells required on average longer bars for consistent drive than did end-free cells of other classes, some of which had restricted length summation. This would seem to be a more plausible explanation for the somewhat weaker suppression of responses to bars of suboptimal length observed in S-cells than in end-free cells in other classes, rather than postulating that S-cells receive a relatively weaker noise-sensitive inhibitory input.

7.2. MODULATORY INFLUENCE OF A MOVING NOISE BACKGROUND ON BAR-EVOKED RESPONSES AS A FUNCTION OF STIMULUS VELOCITY

The results presented thus far were obtained with the bar and the noise background moving at the same velocity, close to the optimum for an oriented stimulus. It was of some interest to explore the suppressive influence of synchronously moving noise backgrounds as a function of stimulus velocity, particularly since it has been reported (Orban et al., 1981a, and see discussion in Bishop et al., 1980) that at least in velocity tuned (VT) cells percent end-zone inhibition is maximal at the preferred velocity for a bar of optimal length. If the magnitude of response suppression exerted by moving noise backgrounds were similarly dependent on stimulus velocity, the experiments described in the previous section would have revealed in each cell the maximum suppression of response to a bar of fixed length. Indeed, background motion may have had little or no influence on responses to short bars moving at some non-optimal velocities. Conversely, synchronous motion of the noise background might conceivably produce a linear

subtractive change in firing rate, and thus percent suppression would be maximum not at the preferred velocity, but for the velocity at which the bar evoked the weakest criterion response(s). A third possibility is that synchronous background motion induces a divisive-like change in firing rate, in which case percent suppression would remain relatively constant irrespective of the strength of the criterion response, and would thus be invariant with stimulus velocity.

In order to investigate the modulatory influence of synchronous background motion as a function of velocity, the following strategy was adopted. The experiment described in section 7.1 was performed initially on each cell. Subsequently, an optimally-oriented bar of fixed width and length was swept in both directions along the axis orthogonal to its orientation, alternately in synchrony with its noise background in the same direction and with the same phase, velocity and amplitude of motion, and independently across the same stationary noise background. Stimulus velocity was systematically varied and the order of testing with different velocities was randomized. Note that this is quite different from the stimulus configuration used at least in part by others working in the cat visual cortex (Hammond and MacKay, 1981b; von Grunau and Frost, 1983; Hammond and Smith, 1984; Hammond et al., 1986), whereby the velocity of the bar stimulus was fixed close to the optimum for each cell, while that of the noise background was systematically varied.

In preliminary experiments, the influence of stimulus velocity on the suppressive effects of synchronously moving noise backgrounds was investigated using comparison bars of different length. It became apparent, however, that when the difference in response to the bar and the combination stimulus was small, the data points representing percent suppression as a function of velocity showed considerable scatter and no meaningful conclusions could be drawn. Thus, in subsequent experiments, the following strategy was adopted. On the basis of results from the experiment described in section 7.1, a comparison bar was selected which, when moving at the preferred velocity, was short enough to reveal substantial suppres-

sion by moving noise backgrounds, but which at the same time would be expected to elicit consistent drive throughout most of the effective velocity range, and thus provide a good criterion for comparison with the response to the combination stimulus. Because of the need for a consistent criterion response over a wide range of velocities, quantitative comparisons were restricted in the vast majority of cells to motion in the preferred direction. In others, however, results were consistent for the preferred and opposite directions of motion. For technical reasons, velocities above 200 /sec were not used, and responses to the slowest velocities could not be tested, since stimulus excursion always exceeded minimum response field width and maximum sweep time was 1sec (see Methods). Nevertheless, as can be seen in Fig. 7.4 and Fig. 7.5 (upper row), which show comparable results for end-free and end-stopped cells respectively, comparisons between responses to the bar and the combination stimulus were made over most of the effective velocity range in each cell. Velocity tuning *per se* was not of primary interest, since it has been investigated extensively by others in area 18 (Riva Sanseverino et al., 1979; Orban et al., 1981a). However, the number and range of velocities covered was sufficient to define velocity-response functions according to Orban et al. (1981a). At the same time, neglect of the lower and upper limit of velocity tuning meant that at all velocities used, response to bars of suboptimal length provided a good criterion for comparison with the combination stimulus.

7.2.1. End-Free Cells

Typical results are illustrated in Fig. 7.4, which shows in 3 end-free cells velocity-response functions for interleaved presentation of a bar and the combination stimulus, together with the ratio of response to the bar moving at a fixed velocity, with its noise background alternately moving and stationary. Although there was a certain amount of scatter of the data points, particularly when the criterion response was small, the relative response to the combination stimulus was essentially invariant with velocity in all cells. (Note that the curves fitted to the

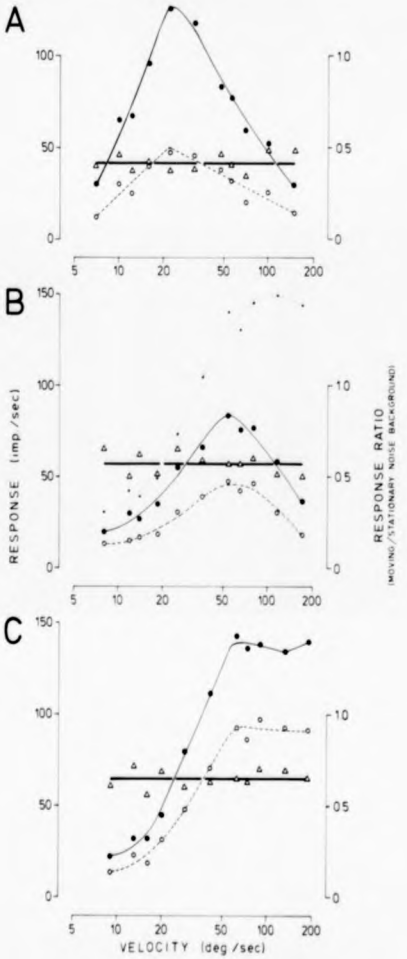
A
B
C
100
50
0
150
1.0
0.5
5
10
20
50
100
200
RESPONSE (imp/sec)
RESPONSE RATIO
(MOVING/STATIONARY NOISE BACKGROUND)
VELOCITY (deg/sec)

Fig. 7.4. Suppressive influence of moving noise backgrounds on moving bar responses of end-free cells, as a function of the logarithm of stimulus velocity. Comparison of response to an optimally-oriented moving bar of fixed length and width but variable velocity, swept in the preferred direction, alternately in synchrony with a background of visual noise, with the same phase, velocity and amplitude of motion (open circles; combination stimulus) and independently across the same stationary noise background (filled circles). Thin continuous and broken lines are the velocity-response curves for the bar and the combination stimulus respectively, fitted by eye. Response derived from PSTHs (16 presentations) and expressed as peak firing frequency (averaged over the 3 adjacent bins containing the highest spike count), subtracted from spontaneous activity assessed at the time each PSTH was compiled. Triangles indicate the ratio of response (right vertical scale) to the bar moving at a fixed velocity, with the noise background alternately moving and stationary. Thick solid line is the by-eye fit to the data points. *A*: C-cell with restricted length summation. Bar length 1°, limit value of length summation 1·5°, minimum response field width 2·5°, bar width 0·6°, stimulus excursion 7°. The cell is velocity tuned, with a preferred velocity of around 25°/sec. Note that synchronous motion of the noise background reduces the ascending and descending slopes of the velocity-response function. Response reduction is greatest at the preferred velocity, but the relative response to the combination stimulus, and hence percent suppression (around 60%), is essentially invariant with velocity. *B*: S-cell with dissimilar velocity-response functions for bars of optimal and suboptimal length, a feature of end-free cells with substantial length summation. For an optimal-length bar (6°), the cell has a VHP function, with a preferred velocity of around 100°/sec (dotted line fitted to crosses), which is much higher than that for a 3·5°-long bar (around 55°/sec). Minimum response-field width 1·9°, bar width 0·5°, stimulus excursion 8°. Percent suppression of response to a 3·5°-long bar (around 45%) is essentially invariant with velocity. *C*: Length-summating C-cell whose response to a bar of optimal length (8·5°, limit value of length summation) is substantially suppressed by synchronous motion of the noise background. Minimum response field width 4·9°, bar width 0·8°, stimulus excursion 9°. For the comparison bar, the cell has a VHP function with a wide dynamic range. Synchronous motion of the noise background reduces the slope of the velocity-response function. Percent suppression (around 35%) is essentially invariant with velocity. Note that in all cells, the inhibitory effect of synchronously-moving noise backgrounds would seem to be divisive rather than subtractive.

triangular symbols representing response ratio are not precise interpolations, but the best-fitting *horizontal* lines). Comparisons in Fig. 7.4*A* are for a C-cell with restricted length summation. The criterion response was obtained using a bar of suboptimal length (1°), for which the cell was velocity tuned, with a preferred velocity of around 25°/sec. Velocity tuning for a bar of optimal length (not illustrated) did not differ substantially from that for a bar of suboptimal length. The response to a bar of suboptimal length was significantly depressed by motion of the noise background, but not by an equal amount at all velocities. Synchronous motion of the noise background reduced the ascending and descending slopes of the velocity-response function. The relative response to the combination stimulus, and hence percent suppression, were essentially invariant with velocity.

Comparable results are illustrated in Fig. 7.4*B* for an S-cell which showed substantial length summation. When stimulated with a bar of suboptimal length (1.5°), the cell was rather broadly tuned for velocity (thin, continuous line fitted to filled circles), with an optimum of around 35°/sec. Synchronous motion of the noise background was seen to reduce the ascending slope of the velocity-response function, though the effect was not as dramatic as in Fig. 7.4*A*, where the criterion response had a much wider dynamic range. The results from this cell were obtained in initial experiments in which the influence of velocity on the suppressive effects of the synchronously moving noise background was investigated using comparison bars of different length. It was thus possible to compare the velocity-response function for a bar of suboptimal length with that for a bar of optimal length (6°; dotted line fitted to crosses). The cell had a velocity high-pass (VHP) function for a bar of optimal length, and a higher preferred velocity (around 100°/sec) than for a bar of suboptimal length. The velocity-response function for a bar of optimal length also had a relatively wider dynamic range, the difference in response to the short and the long bar being greater at high than at low velocities. Comparable results obtained in all VHP cells with substantial length summation for which velocity-response functions were derived with bars of optimal and suboptimal length. In addition, when stimulated with bars of suboptimal length,

VT cells tended to have more broad-band functions, while velocity broad-band (VBB) cells themselves could show velocity low-pass (VLP) curves. The sample of cells in which velocity-response functions were derived using bars of optimal and suboptimal length was small, since it was not the primary aim of the present study to investigate the influence of bar length on velocity selectivity. However, the present incidental observations indicate that at least in end-free cells showing substantial length summation, preferred velocity and velocity-response functions may be dependent on bar length. This implies, conversely, that length-response functions for a moving bar may vary with velocity of motion.

Finding that a longer bar tended to yield a more realistic velocity-response function with a wide dynamic range, the longest comparison bar was chosen which was consistent with substantial response suppression by moving noise backgrounds. Occasionally, a cell would show marked suppression of response to a bar of optimal length. An example is seen in Fig. 7.4C, which shows the suppressive influence of synchronous motion of the noise background as a function of velocity, in a C-cell with a VHP function for a bar of optimal length (8.5°). Synchronous motion of the noise background reduced the ascending slope of the velocity-response function, response depression remaining relatively constant once the criterion response had reached an asymptotic value. As in all other end-free cells, percent suppression was essentially invariant with velocity.

Note that the present results contrast with those from the 4 noise-sensitive cells in which comparable measurements were made. In these cells, percent *enhancement* of response to a moving bar by synchronous motion of its noise background was (understandably) strongly dependent on stimulus velocity. In each cell, response enhancement was observed only for stimulus velocities within the effective range for visual noise moving alone (in the preferred direction for an oriented stimulus). However, percent enhancement was not necessarily maximum at the preferred velocity for noise motion alone but, at a given velocity, seemed to depend on the relative strength of the separate responses to bar and noise motion.

In a few cells which had rather broad-band velocity-response functions for the comparison bar, the criterion response was equally depressed over a wide range

of velocities. An end-stopped example is shown in Fig. 7.5*E* and *F*, and similar results were observed in some end-free cells. A linear subtractive change in firing rate induced by synchronous motion of the noise background could not be excluded as an explanation of the results from these cells. However, the results from the majority of cells in which the criterion response varied with velocity over a wide range, while percent suppression remained relatively constant, suggest strongly that the inhibitory effect of synchronous motion of the noise background on bar responses was divisive rather than subtractive. Note that in all cells illustrated, a response reduction throughout the effective velocity range by an amount comparable to that observed at the preferred velocity would have been sufficient to abolish the response to the combination stimulus at some non-optimal velocities. Pertinently, the generation of cortical orientation specificity (Rose, 1977b; Morrone et al., 1982) and direction selectivity (Dean et al., 1980) would seem to involve divisive rather than subtractive inhibition.

7.2.2. End-Stopped Cells

While in end-free cells percent suppression of response by synchronously moving noise backgrounds is invariant with velocity, it has been reported that in VT cells percent end-zone inhibition is velocity-dependent (Orban et al., 1981a). However, it remains to be demonstrated that the velocity-dependence of end-zone inhibition is a general property of end-stopped cells of all velocity types. On the other hand, it can not be assumed that the velocity-invariance of percent suppression by moving noise backgrounds observed in end-free cells also obtains in their end-stopped counterparts. Nevertheless, the above results introduce the possibility that in end-stopped cells the mechanisms responsible for response suppression by moving noise backgrounds and end-zone inhibition are independent. To test this proposition directly, end-zone inhibition and the suppressive influence of moving noise backgrounds were compared over a wide range of velocities in the same end-stopped cells. Since for technical reasons, interleaved presentation of bars

of different length was not possible, the following procedure was adopted. Comparisons were made between the response to a moving bar and the combination stimulus over a range of velocities, first using a bar of optimal length and subsequently with a 20°-long bar. Thus, in the same cell, the suppression of response to a bar of optimal length by motion of its noise background could be compared over a range of velocities with *maximum* end-zone inhibition. Since for stimulus motion at the preferred velocity, the noise background substantially suppressed in all end-stopped cells the response to a bar of optimal length, it was possible to use this as a comparison stimulus to investigate the magnitude of moving noise suppression as a function of velocity. The use of a comparison bar of optimal length had the additional advantage that it yielded a realistic velocity-response curve with a wide dynamic range.

The two C_B-cells and the single A_B cell had VHP functions for bars of optimal length. Of the 3 S_B-cells, 2 were VT and the other had a VBB function. Representative results for each of these velocity types are shown in Fig. 7.5, which compares in a C_B cell (*A* and *B*) and two S_B-cells (*C* and *D*, *E* and *F*), response suppression by moving noise backgrounds (upper row) with end-zone inhibition (lower row) as a function of stimulus velocity. In all end-stopped cells, percent suppression exerted by synchronous motion of the noise background was essentially invariant with velocity. In VHP (Fig. 7.5*A*) and VT (Fig. 7.5*C*) cells, synchronous motion of the noise background caused a reduction in the slope(s) of the velocity-response function, indicative of a divisive rather than a subtractive change in cell firing rate. In the same cells, however, percent end-zone inhibition was velocity-dependent. In the VHP C_B-cell (Fig. 7.5*B*), percent end-zone inhibition increased with velocity, there being no response to a long bar moving at the preferred velocity for a bar of optimal length. Percent end zone inhibition was also maximal at the preferred velocity for a bar of optimal length in the VT, S_B-cell (Fig. 7.5*D*). The present results confirm and extend those of Orban et al. (1981a), and are in line with other work demonstrating the stimulus inter-dependence of discharge region excitation and end-zone inhibition. Thus Orban et al. (1979b)

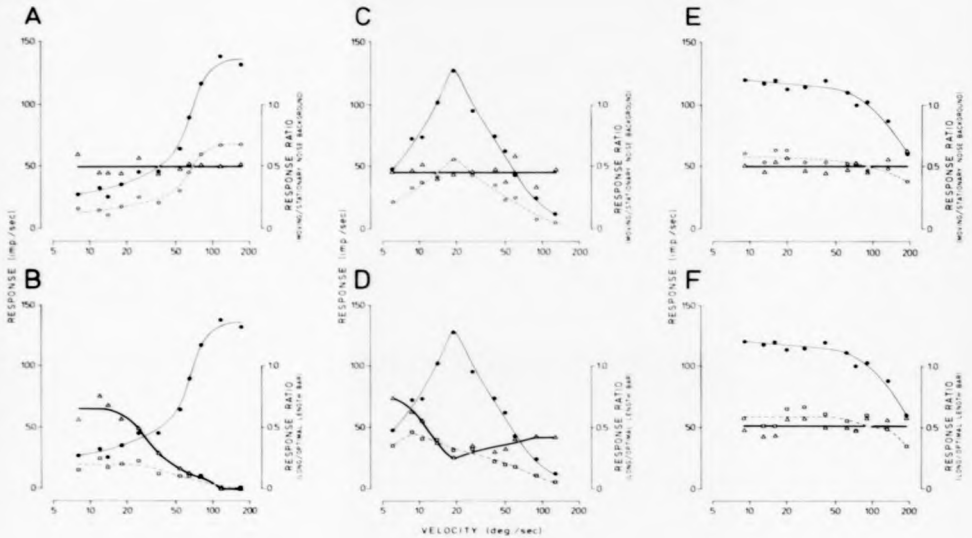
A
B
C
D
E
F
RESPONSE (imp/sec)
RESPONSE RATIO
VELOCITY (deg./sec)

Fig. 7.5. Comparison of response suppression by synchronously moving noise backgrounds (upper row) with end-zone inhibition (lower row) as a function of the logarithm of stimulus velocity, in each of 3 end-stopped cells (*A+B*, *C+D*, *E+F*). Upper functions: conventions and derivation as in Fig. 7.4, except that bar length was set optimally for each cell. Lower functions: the velocity-response curve for a bar of optimum length is transposed from the appropriate upper function for comparison with that for a 20°-long bar (broken lines fitted to square symbols). Results for a 20°-long bar were derived in precisely the same manner as those for a bar of optimal length. For the long bar, responses are plotted only for motion against a stationary noise background. Triangles represent the ratio of response to the long and to the optimal length bar moving at the same velocity. Thick, solid lines are the by-eye fits to the data points. *A+B*: C_B-cell with a VHP function for a bar of optimal length (2·5°). Minimum response field width 4·8°, bar width 0·8°, stimulus excursion 8°. The relative response to the combination stimulus remains rather constant (at around 0·5) with stimulus velocity, whereas the relative response to the long bar declines as velocity is increased, there being no response to a long bar at the preferred velocity for a bar of optimal length. Thus, percent suppression of bar response by synchronous motion of the noise background is essentially invariant with velocity, while percent end-zone inhibition is velocity-dependent. *C+D*: S_B-cell, velocity tuned for a bar of optimal length (1°). Minimum response field width 2·0°, bar width 0·7°, stimulus excursion 6°. Percent suppression of bar response by synchronous motion of the noise background (around 55%) is essentially invariant with velocity, while percent end-zone inhibition is maximal at the preferred velocity for a bar of optimal length. *E+F*: VBB, S_B-cell, same cell as in Fig. 7.3C+*D*. Optimal length bar 1·5°, minimum response field width 2·3°, bar width 0·8°, stimulus excursion 9°. Percent suppression by synchronous motion of the noise background and percent end-zone inhibition (both around 50%) are essentially invariant with velocity. Note however that in this case, the response to the comparison bar remains relatively constant with velocity over a wide range.

reported that end-zone inhibition is orientation-sensitive, being maximal along a cell's receptive field axis orientation. More important in the present context, however, the results indicate that the mechanisms responsible for end-zone inhibition and response suppression by moving noise backgrounds are independent, since in the same end-stopped cells percent suppression by moving noise backgrounds is invariant with velocity, while percent end-zone inhibition is velocity-dependent.

In the VBB, S_H-cell (Fig. 7.5*E* and *F*), both the response suppression caused by synchronous motion of the noise background and end-zone inhibition were essentially invariant with velocity. The possibility that in this cell synchronous motion of the noise background induced a linear subtractive change in firing rate can not be excluded, since the criterion response remained relatively constant with velocity over a wide range. By the same token, the velocity-invariance of end-zone inhibition in this cell suggests that the magnitude of end-zone inhibition is not dependent on stimulus velocity *per se*, but is related to the magnitude of discharge region excitation.

CHAPTER 8

DISCUSSION

8.1. NOISE SENSITIVITY OF CELLS IN AREA 17 AND AREA 18

8.1.1. Encounter Frequency Of Different Cell Types

The encounter frequency of cells in each class was comparable in areas 17 and 18. C-cells formed the majority of encountered units. S-cells were encountered rather less frequently than B-cells, and A-cells formed only a small minority. The high proportion of C-cells sampled in the present study contrasts markedly with reports that S-cells predominate in both areas 17 and 18, with C-cells comprising some 30% of the population (Henry et al., 1979; Bullier and Henry, 1979c; Harvey, 1980a; Orban and Kennedy, 1981; Martin and Whitteridge, 1984). However, for a number of reasons, noise-sensitive C-cells in both areas 17 and 18 are probably numerically less frequent than their proportions in the present samples suggest.

Stereotaxic co-ordinates for recordings in area 17 were chosen with the intention of sampling a high proportion of strongly noise-sensitive C-cells, which are located deep in the superficial layers, but predominantly in layer V (Hammond and MacKay, 1977; Hammond, 1978c; Hammond and Reck, 1980b; Wagner et al., 1981; Hammond and Smith, 1982, 1983, 1984). Long penetrations were made down the medial bank of the lateral gyrus during which the electrode sampled layers I-VI in sequence, but typically remained within the deep layers for many hundred μm. The distribution of C-cells peaks in layer V, where they form the majority of cells (Leventhal and Hirsch, 1978; Henry et al., 1979; Bullier and Henry, 1979c; Orban and Kennedy, 1981; Martin and Whitteridge, 1984). Thus, the choice of penetration co-ordinates would partially explain the over-representation of C-cells, and account for the heavy bias in favour of those from the deep layers. In area 18, the electrode sampled layers I-VI in sequence before entering the white matter. Thus, compared with area 17, C-cells formed a slightly lower proportion of recorded units, and the sample of C-cells contained a much higher proportion of superficial-layer cells. The encounter frequency of cells in both areas 17 and 18 was additionally biased by an intentional search for strongly noise-sensitive units. In

particular, a field of moving noise was frequently employed as the sole search stimulus in an attempt to selectively isolate noise-sensitive cells. Finally, the proportion of cells in different classes was almost certainly biased by electrode sampling. In area 17, the depth at which strongly noise-sensitive cells were encountered, and their ease of isolation led Hammond and Smith (1984) to suggest that they are large pyramidal cells at the base of layer III and in layer Vb. In the present study Group I C-cells in areas 17 and 18, and particularly those in the deep layers, were relatively easy to isolate even with rather low impedance electrodes. Thus strongly noise-sensitive cells in both areas may be large cells. In area 18, C-cells predominate in layer V (Harvey, 1980a; Orban and Kennedy, 1981), which contains many large pyramidal cells (Otsuka and Hassler, 1962; Garey, 1971; Harvey, 1980a; Humphrey et al., 1985b). In the superficial layers Group I C-cells may be the large pyramidal cells on the border between layers III and IV, or the large loosely-packed pyramidal cells which are prevalent some 200μm above this border (Humphrey et al., 1985b).

8.1.2. Comparisons Of Noise Sensitivity In Areas 17 and 18

The most significant general feature of the results presented in Chapter 5 was the overall similarity between areas 17 and 18 in terms of the noise sensitivity of different cell types, and the association for cells within a class between noise sensitivity and receptive field properties. In each cortical area, comparable differences in response properties were observed between different cell classes, though variations in response properties were observed among cells in a given class which were associated with responsiveness to moving noise.

The similarity in the noise sensitivity of areas 17 and 18 depended on the use of a noise field with an appropriate grain size for cells in the two areas; due to the poorer spatial resolution in area 18, it was necessary to use a larger grain-size noise field in this area to demonstrate the noise sensitivity of Group I and Group II cells (those whose responses to noise were independent of the "structure" in the

noise sample). At the same time, however, a comparison of Tables 5.1 and 5.4 shows that, although a larger grain-size noise field was used to study area 18, the proportion of Group III ('structure-sensitive') cells compared with Group IV ('noise-unresponsive') cells was similar in the two areas. It should also be noted that, while the receptive field eccentricity groupings were different in areas 17 and 18, the range of receptive field eccentricities of the cells in the two areas was broadly comparable. Thus, 72% of cells recorded in area 18 had receptive fields within the eccentricity range of those recorded in area 17 (0-10°), and 87% had receptive fields within 12° of the area centralis projection. Only 22% of C-cells in area 18 had receptive fields in the range 10-18°, and there was no evidence of an increase or decrease in noise sensitivity of C-cells with receptive field eccentricity. Significantly, however, all S- and B-cells in area 18 which responded to noise motion *per se*, rather than to the individual elements in the noise sample, had receptive fields located more than 10° from the area centralis projection (see section 8.1.3.).

(a) Cell Class And Noise Sensitivity

Considering areas 17 and 18 together, most C-cells (72%) were noise-sensitive and the majority (59%) belonged to Group I. The lower proportion of noise-sensitive C-cells in area 18 compared with area 17 could be attributed to the relatively higher proportion of area 18 C-cells recorded in the superficial layers. However, the difference in the proportion of noise-sensitive C-cells in the two cortical areas or in the deep and superficial layers of area 18 was not statistically significant. In both areas, a significant proportion of C-cells was sensitive to the 'structure' in the noise sample and in area 18 some were completely unresponsive to moving noise. Nevertheless, C-cells comprised the vast majority (86%) of noise-sensitive cells, and Group I cells belonged almost exclusively (93%) to the C family.

The second highest proportion of noise-sensitive cells (33%) was found among B-cells. However, whereas most (80%) noise-sensitive C-cells belonged to Group I

the majority (60%) of noise-sensitive B-cells occupied Group II. Compared with their counterparts in area 17, a relatively higher proportion of B-cells in area 18 was noise-sensitive, though this difference was not statistically significant. In area 18, as in area 17 (cf. Henry, 1977; Henry et al., 1978b), B-cells tended to have narrower directional tuning and lower spontaneous activity than C-cells. It should be emphasized, however, that the present classification scheme (see Chapter 5) was not identical to that of Henry (1977) and Henry et al. (1978b). Thus, the single B-cell recorded with relatively high spontaneous activity and broad directional tuning would probably not have been so classified by Henry et al. (1978b), although it did exhibit a sharply peaking response profile to a moving bar. Moreover, the distinct lack of correlation between level of spontaneous activity and width of directional tuning in a further two B-cells would have precluded an unequivocal assignment to the B- or the C-class according to the criteria of Henry (1977) and Henry et al. (1978b). Significantly, in both cortical areas, noise-sensitive B-cells had higher spontaneous activity and wider receptive fields than their noise-insensitive counterparts.

Of the twenty-four S-cells recorded from areas 17 and 18, only three were noise-sensitive, though one area 18 S-cell responded vigorously to moving noise. In addition to their relative insensitivity to moving noise as a group, S-cells in both areas were characterized by low or absent spontaneous activity and narrow directional tuning. The vast majority of S-cells were direction selective and strongly dominated by one or other eye. The distinguishing feature of the noise-sensitive S-cell in area 17 was its relatively wide receptive field, while noise-sensitive S-cells in area 18 had peripheral receptive fields and were unique among S-cells in being spontaneously active. Only 5 A-cells were recorded in areas 17 and 18. They were more broadly tuned for direction than S-cells and unresponsive to moving noise.

Area 17

The results on the noise sensitivity of different cell types in area 17 are broadly con-

gruent with previous reports that in striate cortex only complex cells respond to moving texture and that, with respect to their noise sensitivity, complex cells form a rather heterogeneous group (Hammond and MacKay, 1975, 1977; Hammond, 1978*c*; Hoffmann et al., 1980; Hammond and Smith, 1982, 1983, 1984). Hammond and MacKay (1975, 1977) found that the weak response of a small minority of simple cells to a moving field of texture was related to the non-uniformities of grain density in a particular sample. More recently Morrone et al. (1982*a*), while confirming that simple cells are weakly sensitive to motion of partially correlated 2-D noise, also found that some 20% of simple cells responded to motion of random 2-D noise. Since their noise-sensitive simple cells were recorded predominantly in preparations in which cells had high spontaneous activity and properties associated with deep levels of anæsthesia, such as broad orientation and spatial frequency tuning, and transient responses to stationary flash-presented bars (Ikeda and Wright, 1974), they suggested that the differences in simple-cell responsiveness to noise might reflect varying states of anæsthesia. In the present study the single noise-sensitive S-cell recorded in area 17 did not differ substantially from its noise-insensitive counterparts in directional tuning or level of spontaneous activity, and was encountered during the first recording session. Thus, the noise sensitivity of this S-cell would not seem to reflect deep anæsthesia, nor could it be attributed to deterioration of the preparation. Thus, the possibility that area 17 simple cells do not form a homogeneous group with respect to noise sensitivity cannot be excluded, although it should be emphasized that, since tests for spatial summation within receptive field subregions were not carried out, S-cells in the present study did not correspond directly with simple cells as classified by Hubel and Wiesel (1962). Similarly, spatial summation within and antagonism between the receptive field subregions of simple cells in Morrone et al.'s (1982) study were not demonstrated directly, but inferred from the modulation pattern to a drifting sine-wave grating.

Skottun et al. (1985) have claimed in a short report that many simple cells give a response to moving noise which is unrelated to the individual elements in the

noise sample, while many complex cells are noise-insensitive. This is difficult to reconcile with the present results and those of others (Hammond and MacKay, 1975, 1977; Hammond, 1978c; Hoffmann et al., 1980; Hammond and Smith, 1982, 1983, 1984) on the noise sensitivity of cells in area 17. One possible source of discrepancy is the classification scheme employed by Skottun et al. (1985). Cell classification was based on the presence or absence of modulation of response to a drifting sine-wave grating, and the degree of response modulation alone does not classify all neurones unequivocally as simple or complex (Pollen et al., 1978; Glezer et al., 1980; Kulikowski and Bishop, 1981, 1982; Dean and Tolhurst, 1983). A further consideration, which applies to all studies of noise sensitivity of cortical cells, is level of anæsthesia. Area 17 complex cells with the strongest sensitivity to noise are located in the deep layers (Hammond and MacKay, 1977; Hammond, 1978c; Hammond and Smith, 1983, 1984) and, during slow-wave sleep, activity in the deep layers is depressed compared with that in the superficial layers (Livingstone and Hubel, 1981). Moreover, in the present study, the response to moving noise could often be selectively improved by lightening anæsthesia as far as was consistent with monitoring criteria indicative of a satisfactory behavioural state. On the other hand, the broadening of orientation and spatial frequency tuning of cortical cells during deep anæsthesia (Ikeda and Wright, 1974) suggests a weakening of the effects of intracortical inhibition, and there is evidence that simple-cell insensitivity to noise is due to intracortical inhibition (see below). Thus deep anæsthesia probably renders simple cells more and complex cells less sensitive to moving noise.

The weak noise sensitivity of area 17 B-cells (Hammond and Smith, 1982, 1983, 1984) was confirmed in the present study, though one B-cell was found in Group I. Since, among B-cells, it had a relatively wide receptive field and high spontaneous activity, it may have been classified as a 'conventional' complex cell by Hammond and Smith (1982, 1983, 1984). These complex cells and C-cells in the present study showed the greatest sensitivity to moving noise as a group, but substantial variation in noise sensitivity which was associated with secondary response

properties (Hammond and Smith 1983, 1984, and see below).

Area 18

The present study represents the first attempt to compare the noise sensitivity of area 17 and area 18 cells with receptive fields at comparable eccentricities, using identical animal preparation, experimental procedure, visual stimulation and cell classification. For a variety of reasons outlined in the Introduction, results from the small number of studies, in which various types of 2-D random patterns have been used as stimuli in area 18, are not directly comparable with the present results or those of previous studies of noise sensitivity of area 17 cells (Hammond and MacKay, 1977, 1977; Hammond and Smith 1982, 1983, 1984). However, most authors (Orban et al., 1975; Orban and Callens, 1977a; Gibson et al., 1978; Schoppmann, 1981; Hoffmann et al., 1984) have reported the existence of cells in area 18 which respond to 2-D random stimuli and, using the same random noise stimulus as in the present study, Hammond and MacKay (1977) found excellent texture response in cells recorded incidentally from area 18. Dinse and von Seelen (1981b), on the other hand, reported that area 18 cells respond weakly or not at all to motion of Gaussian noise. In this study, the absence of response to moving noise cannot be attributed to excessively deep anaesthesia, since animals were maintained on nitrous oxide/oxygen mixtures alone during recording sessions and used as the sole anaesthetic, nitrous oxide is inadequate to maintain anaesthesia in cats (Richards and Webb, 1975; Hammond, 1978a,b). Dinse and von Seelen (1981b) suggest that the relatively weak noise sensitivity they found in area 18, compared with that reported by Hammond and MacKay (1977) and Orban and Callens (1977a), reflects the different spatial frequency ranges of the noise processes used in different studies. One assumes that the spatial frequency of the Gaussian noise used by Dinse and von Seelen (1981b) was too high for area 18 cells.

The closest parallel with the present study is that of Orban and Callens (1977a)

who reported that in area 18, simple cells give little or no response to motion of a random square pattern which drives both end-free and end-stopped complex cells. However the two studies are not directly comparable. Orban and Callens' (1977a) cells were recorded in the peripheral projection of area 18 (receptive field eccentricity 10-50°), whereas the receptive fields of most units in the present study were in the range 5-10°, and none was located more than 18° from the area centralis projection. Further, the large element size (1° × 1°) in the pattern used by Orban and Callens (1977a), while presumably reflecting the receptive field size of recorded units, contrasts markedly with the average grain size (8') of the present visual noise stimulus. Finally, Orban and Callens (1977a) did not use stationary flash-presented stimuli to classify cells, and thus could not distinguish between simple and B-cells. Nevertheless, Orban and Callens' (1977a) finding that cells which give a modulated response to a drifting sine wave grating and have low spontaneous activity and inhibitory sidebands respond weakly to motion of a random square pattern is in line with the weak noise sensitivity of most S- and B-cells in the present study. Moreover, Orban and Callens (1977a) report that, among cells with inhibitory sidebands, the relative response to a random pattern (compared with the response to a moving grating) was related to level of spontaneous activity. Among area 18 S- and B-cells in the present study, those sensitive to noise were unique in being spontaneously active, and the Group I B-cell had high resting discharge. Since Orban and Callens' (1977a) complex cells lacked inhibitory sidebands, and thus almost certainly did not include B cells, they probably correspond closely to the C-cells of the present study. Both studies agree that this cell type shows the greatest sensitivity to noise, although a minority of C-cells in the present sample were insensitive to noise.

(b) C-Cells: Noise Sensitivity And Response Properties

In each area, C-cells had the broadest directional tuning and the highest spontaneous activity. In addition, a similarly high proportion of C-cells in the two

cortical areas was direction-selective or received good binocular drive. Substantial differences in response properties of C-cells were found not between those sensitive and insensitive to noise, but between Group I cells and the remaining C-cells. Group I C-cells in areas 17 and 18 were strikingly similar in response properties. Among C-cells, they had relatively broad directional tuning and contained a relatively high proportion of direction-selective and binocularly-driven cells. Indeed, the vast majority of C-cells which were direction-selective or which received comparable drive through either eye were found in Group I. None of these differences could be attributed to pooling cells with receptive fields in different eccentricity classes. In general, the important determinant of response properties was group membership rather than whether a cell was encountered in the superficial or deep layers. However in area 18, the proportions of binocularly-driven and direction-selective cells among C-cells in Group I was higher for deep-layer cells considered separately.

The only significant difference in the response properties of Group I C-cells in the two cortical areas was in level of spontaneous activity. Group I C-cells in area 17 had higher spontaneous activity than their counterparts in area 18, but in both areas, C-cells in Group I had higher spontaneous activity than other C-cells. In area 18, deep-layer C-cells had higher spontaneous activity than superficial-layer C-cells. The relatively high spontaneous activity of Group I C-cells in area 18 did not simply reflect the high proportion of deep layer C-cells they contained. It should be emphasized that high spontaneous activity was a real attribute of Group I C-cells: they were often recorded early in an experiment and in the same penetration as cells with low or absent spontaneous activity and poor noise sensitivity. On the other hand, the possibility that the good noise sensitivity of Group I C-cells simply reflected a high overall level of excitability, for example as a result of damage by the electrode, could be excluded. On the contrary, irrespective of cell type, a rapid, dramatic increase in spontaneous activity was always associated with a *decrease* in responsiveness. In any event, assignment to groups I-IV was made on the basis of *relative* preference for noise and bar

stimuli. Although cortical cells may well receive separate bar and noise inputs (see section 8.3.2), one would not expect damage to Group I cells to lead in every case to a relative improvement in response to moving noise.

There was some indication that among C-cells' responsiveness to moving noise was associated with receptive field width. In area 18, only those superficial-layer C-cells with the widest receptive fields were found in Group I. In area 17, the noise-insensitive superficial layer C-cells had conspicuously narrow receptive fields, while among deep-layer C-cells, those in Group II had narrower receptive fields than those in Group I. Most C-cells with restricted length summation were found in Group I. Localized length summation, however, was not a necessary condition for good noise sensitivity of C-cells, nor did the presence of end-inhibition preclude vigorous responsiveness to moving noise.

Area 17

The finding that group membership (on the basis of responsiveness to moving noise) was the important determinant of receptive field properties of area 17 C-cells seems at variance with reports (Leventhal and Hirsch, 1978; Hammond and Smith, 1983, 1984) that, compared with superficial-layer complex cells, those in the deep layers have relatively large receptive fields, high spontaneous activity and broad directional tuning, and more often receive comparable drive through either eye. Bishop et al. (1980) also found that deep-layer complex cells had higher spontaneous activity than those in the superficial layers. The interlaminar differences in complex cell properties reported by Leventhal and Hirsch (1978) and Bishop et al. (1980) may be attributable in part to the inclusion in the sample of superficial-layer complex cells of B-cells, which have low spontaneous activity, small, sharply tuned receptive fields, and are predominantly monocularly-driven (Henry, 1977; Henry et al., 1978b; Orban and Kennedy, 1981; Hammond and Smith, 1984). However, in a sample of noise-sensitive complex cells which largely excluded B-cells, Hammond and Smith (1983, 1984) found that those in the deep

layers were more broadly tuned for direction and had higher spontaneous activity than those in the superficial layers. Further, in contrast to superficial-layer complex cells, deep-layer complex cells were uniformly direction-selective. The present results are, however, consistent with reports (Hammond and Smith 1983, 1984) that, compared with deep-layer complex cells, those in the superficial layers show greater heterogeneity in response properties, which is to some extent associated with noise sensitivity. In the superficial layers, direction-selective cells show greater sensitivity to noise than bidirectional cells and those with suppression of firing in the non-preferred (null) direction have high spontaneous activity and broad directional tuning (Hammond and Smith 1983, 1984). These latter cells are similar to deep-layer complex cells, which show the greatest sensitivity to noise. In the present study, the number of C-cells in the superficial layers was too small to allow quantitative comparisons with those in the deep layers, but superficial- and deep layer Group I C-cells had comparable properties. Among superficial-layer C-cells, those in Group I had little in common with those in Group III, which had conspicuously small receptive fields, narrow directional tuning and low spontaneous activity, and which were monocularly driven and bidirectional for bar motion, and showed substantial length summation. This is consistent with the finding that in area 17, superficial-layer complex cells which gave a negligible response to moving noise, had small, sharply tuned receptive fields, showed substantial length summation, and had low spontaneous activity (Hammond and Smith 1984).

The present finding that deep layer, Group I C-cells in area 17 had broad directional tuning and high spontaneous activity, and were predominantly direction-selective and binocularly driven is consistent with previous descriptions of strongly noise-sensitive, deep layer complex cells in striate cortex (Hammond and Smith 1983, 1984). However, Hammond and Smith (1983, 1984) reported that all end-free complex cells in the deep layers were strongly sensitive to noise, whereas, in the present study, 30% of deep-layer C-cells were found outside Group I, and only one of these was end-stopped. The insensitivity to noise of this cell is unlikely

to be due to the presence of end-zone inhibition, since Hammond and Shorrocks (1987) have recently reported that end-stopped cells show little evidence of end-inhibition when tested with moving texture. The deep-layer C-cells with weak sensitivity to noise may be layer VI cells, which were recorded rarely by Hammond and Smith (1983, 1984) (see Hammond and Ahmed 1985) and have uniformly low spontaneous activity and sharp directional tuning (Weyand et al. 1986), narrow receptive fields within which there is substantial length summation (Gilbert 1977) and are predominantly monocularly-driven (Ferster 1981).

Overall, the present finding that the vast majority of direction-selective C-cells, and all those in the deep layers, belonged to Group I is consistent with reports that direction-selective complex cells show the greatest sensitivity to moving noise (Hammond and Smith, 1983, 1984) and have broader directional tuning and higher spontaneous activity than direction-biased and bidirectional complex cells (Hammond 1981a).

Area 18

As a group, deep-layer C-cells in area 18 were more sensitive to noise than their counterparts in the superficial layers. Thus, although there was no significant difference between the proportions of noise-sensitive C-cells in the deep and superficial layers, a relatively higher proportion of deep-layer C-cells belonged to Group I. Moreover, among noise-sensitive cells, deep-layer C-cells were confined to Group I, whereas superficial-layer C-cells were distributed evenly between groups I and II. These results parallel the interlaminar difference in noise sensitivity of area 17 complex cells (Hammond and MacKay 1977, Hammond and Smith 1983, 1984) and are consistent with the observation of Orban et al. (1975) who found that in a small sample of area 18 cells, those which responded well to motion of a random square pattern were, on average, encountered deeper in the cortex than other cells. In addition, the association between noise sensitivity and response properties of superficial-layer C-cells in area 18 was comparable to that

reported by Hammond and Smith (1983, 1984) for superficial-layer complex cells in area 17. Among superficial-layer cells, those in Group I had significantly wider receptive fields than other C-cells, thus paralleling the difference between noise-sensitive and noise-insensitive C-cells in area 17 (Hammond and Smith, 1984, present study). Among superficial-layer C-cells, those in Group I had higher spontaneous activity and broader directional tuning than those in other groups, and were predominantly direction-selective with null suppression. This is in line with results from area 17 (Hammond and Smith, 1983, 1984) where, in the superficial layers, direction-selective complex cells showed the strongest sensitivity to noise, and those with null suppression had broad directional tuning and high spontaneous activity. On the other hand among superficial-layer C-cells, the proportion of direction-selective cells was not significantly higher in Group I than in other groups. Thus, as in area 17 (Hammond and Smith, 1983, 1984), both direction selective and bidirectional, superficial-layer C-cells could show weak or negligible responses to moving noise. Among Group I C-cells, those in the superficial layers were more heterogeneous in spontaneous activity than those in the deep layers and, overall, superficial layer C-cells had lower spontaneous activity than deep-layer C-cells. These interlaminar differences paralled those found in area 17 (Leventhal and Hirsch, 1978; Bishop et al., 1980; Hammond and Smith, 1983, 1984), and are consistent with the report (Ferster, 1981) that in area 18 spontaneous activity is higher in layer V than in other layers. As in area 17 (Hammond and Smith, 1983, 1984), the association between noise sensitivity and ocular dominance was stronger for deep- than for superficial layer C-cells. Hammond and Smith (1983, 1984) found that, with one exception, deep-layer complex cells received comparable drive through either eye, whereas a few cells in the superficial layers received strong monocular drive. However in area 17, binocularity prevailed among noise-sensitive complex cells in the superficial layers, whereas in the present study superficial layer noise sensitive C-cells in area 18 were equally likely to receive strong monocular or binocular drive, while only 40% of superficial-layer Group I C-cells received comparable drive through either eye. This reflects the overall difference in ocular dominance of the superficial layers in each area

the majority of cells in the superficial layers of area 17 receive comparable drive through either eye, whereas superficial-layer cells in area 18 are predominantly monocularly-driven (Ferster, 1981).

As in area 17 (Hammond and Smith, 1983, 1984), the association between noise-sensitivity and response properties was stronger for deep-layer C-cells than for those in the superficial layers. Deep-layer Group I C-cells were broadly tuned for direction and all had high spontaneous activity. With one exception, they received comparable drive through either eye and were direction selective. These properties are remarkably similar to those reported for deep layer complex cells with strong noise sensitivity in area 17 (Hammond and Smith, 1983, 1984). There is considerable attraction in the hypothesis that, as in area 17 (Hammond and Smith, 1984), strongly noise-sensitive C-cells in the deep layers of area 18 are confined largely to layer V. Indeed, layer V cells in area 18 which project to the NOT are strongly sensitive to motion of 2-D random noise (Schoppmann, 1981), while area 18 cells which project to the pons respond vigorously to motion of multiple spot patterns (Gibson et al., 1978) and the cortico-pontine projection from area 18 arises from layer V pyramidal cells (Gibson et al., 1976; Albus et al., 1981).

A significant proportion of deep-layer C-cells in area 18 was sensitive to the 'structure' in the noise sample, and some were completely unresponsive to noise. They had lower spontaneous activity than deep-layer, Group I C-cells and narrow directional tuning. Most were monocularly-driven and none was direction-selective. It remains to be determined whether these are predominantly layer V or layer VI cells. On the one hand, Harvey (1980b) claims that layer VI cortico-thalamic C-cells are not obviously distinguishable from layer V cortico-collicular C-cells, while Ferster (1981) reports that, compared with layer V cells, those in layer VI have lower spontaneous activity and more often receive strong monocular drive.

8.1.3. Explanations For The Noise Sensitivity Of Different Cell Types

The weight of available evidence (Garey, 1971; Garey and Powell, 1971; LeVay and Gilbert, 1976; Davis and Sterling, 1979; Hornung and Garey, 1981; Freund et al., 1985a; but see Einstein et al., 1987) suggests that specific afferents to visual cortex make exclusively Type I synapses (Gray, 1959; Colonnier, 1968), which are thought to be excitatory (Eccles, 1964; Uchizono, 1967; Peters et al., 1976). Accordingly, there is little electrophysiological evidence for monosynaptic thalamo-cortical inhibition (Creutzfeldt and Ito, 1968; Toyama et al., 1974; Ferster and Lindstrom, 1983). Thus, since the vast majority of X-, Y- and W-cells in the retina and visual thalamus respond to moving noise (Mason, 1976a,b, 1981; Hoffmann et al., 1980; Ahmed and Hammond, 1983; Hoffmann and Stone, 1985), the differential noise sensitivity of different cell types in areas 17 and 18 would seem to be mediated intracortically. Some non-concentric W-cells in the retina fail to respond to motion of a field of visual noise, due to the presence of a strong inhibitory receptive field surround (Hoffmann and Stone, 1985), but this cell type is extremely rare. By the same token, some 20% of cells in the thalamus show suppression of spontaneous activity to whole-field noise motion, which is associated with the presence of a strong 'suppressive field', but in many cases response peaks are superimposed upon such suppression (Mason, 1976a,b).

Possible explanations for S-cell insensitivity to moving noise are legion. It is known that area 17 S-cells possess inhibitory sidebands (Bishop et al., 1973; Kato et al., 1978; Palmer and Davis, 1981), and Orban and Callens (1977a) demonstrated the presence of sideband inhibition in area 18 cells which were unresponsive to motion of a random square pattern. Hammond (1978c) suggested that a global stimulus such as moving noise is inadequate to overcome the 'sea of inhibition' surrounding the simple cell field, as indicated by evidence following iontophoretic blockade of intracortical inhibition (P. Hammond, D.M. MacKay, A.M. Sillito, unpublished observations). Another possibility is that in S-cells in both area 17 (Hammond and MacKay, 1975, 1977, 1981b) and area 18 (present study), the absence of re-

sponse to moving noise and the suppression of responses to optimally-oriented bar stimuli by in-phase background noise motion are an expression of the same noise-sensitive inhibitory input. On the other hand, it has been suggested (Burr et al., 1981; Morrone et al., 1982) that an inhibitory input at *orientations outside the excitatory bandwidth* of simple cells prevents them responding to motion of 2-D random noise. Simple cells do respond to motion of 1-D noise which contains the same spatial frequencies as the 2-D noise to which they are unresponsive. However, this response is suppressed by stimulation with a second 1-D pattern at any orientation outside the cell's orientation tuning curve. Burr et al. (1981) and Morrone et al. (1982) argue that motion of 2-D noise provides inhibition over a wide range of spatial frequencies and orientations, which is sufficient to overcome the excitation from a subset of energy falling within a cell's orientation and spatial frequency bandwidth. This argument rests on the assumption that, when presented with a 1-D stimulus, simple cells integrate along the axis of optimum orientation. However, Hammond and MacKay (1981a, 1983b) demonstrated that simple cells do not show linear length summation in response to bars composed of segments of opposite polarity; small elements of reversed contrast to a driving oriented stimulus caused either response attenuation much greater than predicted on the basis of linear spatial summation, or total abolition of response. This finding alone would predict the poor sensitivity of simple cells to motion of 2-D noise without postulating the "cross-orientation inhibition" described by Burr et al. (1981) and Morrone et al. (1982). Like area 17 simple cells (Hoffmann and von Seelen, 1978), simple cells in area 18 have high signal-to-noise thresholds for the detection of a moving bar embedded in a field of stationary noise (Dinse and von Seelen, 1981b), suggesting that they too may be intolerant of luminance gradient reversal along the axis of optimum orientation.

Most area 17 simple cells classified qualitatively according to Hubel and Wiesel (1962) show approximately linear spatial summation when tested with quantitative techniques (Movshon et al., 1978a; Andrews and Pollen, 1979; Kulikowski and Bishop, 1981; Dean and Tolhurst, 1983), and thus might not be expected

to respond to motion of visual noise, which results in little or no nett change in flux across the receptive field. Conceivably, noise-sensitive simple or S-cells (Morrone et al., 1982, present study) are those which show the the greatest departure from linearity of spatial summation. In the present study, the noise-sensitive S-cell recorded in area 17 may have been such a non-linear simple cell, since tests for spatial summation within receptive field subregions were not carried out. On the other hand, one would expect the presence or absence and magnitude of response to moving noise in non-linear simple cells to be related to the degree to which they tolerate luminance gradient reversal along the line of optimum orientation (Hammond and MacKay, 1981a, 1983b).

Since the available data from electrical stimulation studies suggest that some 50% of area 17 simple cells are driven by Y afferents (Singer et al., 1975; Henry et al., 1979; Bullier and Henry, 1979a,b,c; Mustari et al., 1982; Martin and Whitteridge, 1984), linearity of spatial summation would not seem to be determined by the functional type of thalamic input. Linear simple cells have completely discrete excitatory and inhibitory receptive field subregions (Movshon et al., 1978a; Dean and Tolhurst, 1983) and, rather than reflecting the spatial organization of the excitatory geniculate input as postulated by Hubel and Wiesel (1962), these subregions would seem to be established by intracortical inhibition: the excitatory discharge centres of simple cells are basically round, rather than elongated in the plane of optimal orientation (Creutzfeldt et al., 1974; Lee et al., 1977; Sillito et al., 1980b) and simple cells lose their discrete ON and OFF subregions during iontophoretic blockade of GABA-mediated intracortical inhibition (Sillito, 1975). The inhibitory input could derive from a simple cell whose receptive field is superimposed on that of its target neurone, but with the sign of each receptive field subregion reversed: such pairs of simple cells have been recorded simultaneously by Palmer and Davis (1981). Alternatively, each subregion could be generated by inhibition from cells with a single ON or OFF receptive field area, as has been demonstrated by cross-correlation techniques (Toyama et al., 1981a,b). Multipolar stellate cells whose axons ramify locally and make type 2 (presumed inhibitory) synapses (LeVay,

1973, Lund et al., 1979; Peters and Regidor, 1981), would seem ideal candidates for providing such inhibition. The inhibition which establishes the discrete, mutually-antagonistic receptive field subregions of simple cells would at the same time prevent them responding to moving noise in the absence of a noise-sensitive inhibitory input.

Since the thalamic input to area 18 derives almost exclusively from Y-afferents, it is generally accepted that cells in this area summate non-linearly. If, however, the noise insensitivity of area 17 simple cells partially reflects their linearity of spatial summation, it can no longer be assumed that S-cells in area 18, which are also largely noise-insensitive, show non-linear spatial summation. Area 18 receives a small but significant X-input (Tretter et al., 1975; Dreher et al., 1980; Harvey, 1980a; Meyer and Albus, 1981b; Humphrey et al., 1985b), and a projection from layer IV spiny stellate cells in area 17 (Meyer and Albus, 1981a), which have simple or S-type receptive fields (Kelly and van Essen, 1974; Lin et al., 1979; Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984). In addition, there is substantial anatomical evidence (Hollander and Vanegas, 1977; Ferster and LeVay, 1978; Leventhal and Keens, 1978; Meyer and Albus, 1981b) for a projection to area 18 from thalamic W-cells, some of which show linear spatial summation (Sur and Sherman, 1982b). Thus, at least some area 18 cells must receive an input from cells showing linear spatial summation, though this does not of course imply that the recipient cell itself summates linearly. Area 17 B-cells are driven by X-afferents (Henry et al., 1983), but show clear non-linearities of spatial summation (Kulikowski and Bishop, 1982). Moreover, cells receiving a convergent linear and non-linear input would be expected to show certain non-linearities of spatial summation. S-type cells in area 18 give a modulated response to a drifting sine-wave grating (Orban and Callens, 1977a). At least in area 17, the degree of response modulation is closely correlated with the degree to which excitatory and inhibitory subregions are discrete, and cells with completely discrete subregions show linear spatial summation (Movshon et al., 1978a; Dean and Tolhurst, 1983). Pertinently, linear spatial summation has been demonstrated in a cell located

in the area 17/18 border region with a large receptive field (Kulikowski et al. 1981), and simple cells classified according to Hubel and Wiesel (1962), which show spatial summation within receptive field subregions, are common in area 18 (Ferster, 1981).

A number of factors may contribute to the relatively weak sensitivity of B-cells to moving noise. There is evidence that, like S-cells, B-cells possess inhibitory sidebands (see Orban, 1984c, as their sharply peaking histogram profiles in response to moving bar stimuli suggest. Indeed, the area 17 complex cells with inhibitory sidebands described by Albus and Fries (1980), and some of the 'simple' cells described by Sherman et al. (1976) (having by their definition inhibitory sidebands) were probably B-cells. It is thus significant that among B-cells in each area, those sensitive to noise had relatively wide receptive fields, which may reflect weak sideband inhibition. The low spontaneous activity of most B-cells suggests that they receive a tonic inhibitory input, possibly from Group I C-cells with high resting discharge. If the tonic inhibition which suppresses spontaneous activity is generated through the same intracortical mechanisms that produce inhibitory sidebands, noise sensitivity might reflect to some extent the balance between excitatory and inhibitory inputs. In this context it is noteworthy that among B-cells those sensitive to noise were unique in being spontaneously active, while Group I B-cells had high resting discharge levels. In area 18, all noise-sensitive B- and S-cells had receptive fields located more than 10° from the area centralis projection. This finding in a small sample of cells conceivably reflects a genuine increase in the noise sensitivity of B- and S-cells with receptive field eccentricity, possibly due to a decline in the effectiveness of intracortical inhibition (see Orban, 1985), it accounts for the slight areal difference in the noise sensitivity of B-cells. B-cells are intolerant of luminance gradient reversal along the axis of optimum orientation (Hammond and MacKay, 1983a) which, as in S-cells, would predict their poor sensitivity to moving noise. The noise sensitivity of B-cells in area 17 may also reflect their spatial summation properties. Area 17 silent periodic cells, which resemble B-cells in secondary response properties, show less pronounced non-linearities of

spatial summation than other complex cells, and respond weakly to moving noise (Kulikowski and Bishop, 1982). Indeed, the available evidence suggests that, at least in area 17, cells can be categorized in ascending order of non-linearity from linear simple cells through non-linear simple cells and B-cells, to the most typical (highly non-linear) C-cells (Movshon et al., 1978a,b; Andrews and Pollen, 1979; Kulikowski and Bishop, 1981, 1982; Dean and Tolhurst, 1983). The noise sensitivity of different cell types may partially reflect this pseudo-continuum of linearity of spatial summation. The non-linear spatial summation of area 17 C-cells, coupled with their relative tolerance of luminance gradient reversal along the axis of optimal orientation (Hammond and MacKay, 1983a, 1985), would predict their strong sensitivity to moving noise. It seems reasonable to suppose that C-cells in area 18 also summate non-linearly, since they give only an unmodulated response to a drifting sine-wave grating (Orban and Callens, 1977a) and receive thalamic input predominantly via Y-afferents (Harvey, 1980a,b). Thus, it is difficult to account for the insensitivity to noise found in a significant minority of C-cells in areas 17 and 18. The same cells in area 18 have their responses to bar motion strongly suppressed by synchronous background noise motion. Thus, in the absence of plausible alternative explanations, the lack of response to noise, and the suppression of bar-evoked responses may be an expression of the same noise-sensitive inhibitory input from Group 1 C-cells (see section 8.1.). The low spontaneous activity of noise-insensitive C-cells suggests that they receive at least a tonic inhibitory input, possibly from Group 1 C-cells which have characteristically high resting discharge.

8.1.4. Group 1 C-Cells: Noise-Sensitive Inputs And Outputs

Since S-cells are, with few exceptions, noise-insensitive (Hammond and MacKay, 1975, 1977; Morrone et al., 1982; present study), they can not provide the sole input to complex cells, as originally postulated by Hubel and Wiesel (1962). However, it is now well established that some complex cells in area 17 receive monosy-

naptic input from the dLGN (Hoffmann and Stone, 1971; Singer et al., 1975; Henry et al., 1979; Bullier and Henry, 1979a,b,c; Henry et al., 1983; Ferster and Lindstrom, 1983; Tanaka, 1983; Martin and Whitteridge, 1984). The differential velocity sensitivity for bar and noise motion in noise-sensitive cells (Hammond and Reck, 1980b; Hammond and Smith, 1983; and see Chapter 6) might suggest that they receive their major noise-sensitive input via the Y-cell system. However, X-, Y- and W-cells in the retina and visual thalamus respond at velocities above the upper cut-off for most area 17 cells (Cleland and Levick, 1974a; Stone and Fukuda, 1974; Lee and Willshaw, 1978; Dreher and Sefton, 1979; Cleland and Harding, 1983; Frishman et al., 1983; Cleland and Lee, 1985; Orban et al., 1985), and the differences in velocity sensitivity of cells in this area would seem to be mediated intracortically (Goodwin and Henry, 1978; Patel and Sillito, 1978; Sillito et al., 1980a; Duysens et al., 1982, 1984, 1985a,b). Moreover, the differences in velocity sensitivity of X- and Y-cells for bar motion are due almost entirely to spatial factors (Hamasaki and Cohen, 1977; Bullier and Norton, 1979b; Lehmkuhle et al., 1980; Lennie, 1980; Cleland and Harding, 1983; Troy, 1983b; Cleland and Lee, 1985), and it is by no means certain that similar differences would obtain for motion of a global stimulus such as moving noise. However, results from electrical stimulation studies do suggest that the Y-cell system provides the major noise-sensitive pathway to Group I C-cells, since C-cells in layer III and some of those in layer V receive monosynaptic input from the dLGN via Y-afferents (Henry et al., 1983; Ferster and Lindstrom, 1983; Martin and Whitteridge, 1984). Martin and Whitteridge (1984) reported that monosynaptically excited cells in the superficial layers tended to be located deep in layer III, as are strongly noise-sensitive complex cells (Hammond and Smith, 1983, 1984). Anatomical studies (Hornung and Garey, 1981; Freund et al., 1985b) have demonstrated that thalamic afferents in layer IV make contact with the basal dendrites of layer III/IV border pyramids and the apical dendrites of some layer V pyramidal cells, while pyramidal cells in layer VI could receive monosynaptic input on their basal dendrites which extend into layer VI (Lund et al., 1979; Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984). In addition, some Y-axons which innervate layer IV have

collaterals which enter layer V (Freund et al. 1985a, Humphrey et al. 1985a). However, the W-input to area 17, which arrives in layer I and at the layer III/IV and IV/V border regions (Leventhal, 1979), may contribute to the noise sensitivity of Group I C-cells. W-cells in the retina (Ahmed and Hammond, 1983; Hoffmann and Stone, 1985) and visual thalamus (Mason, 1976a,b) respond to moving noise, and all W-subtypes including direction-selective cells, project to the dLGN (Cleland et al., 1976; Wilson et al. 1976; Stanford et al. 1980). Pyramidal cells in layers III and V could receive an input from W-afferents on their basal dendrites or via their apical dendrites which branch in layer I (Lund et al. 1979; Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984). Indeed, Dreher et al. (1980) have reported physiological evidence for a direct W-input to many superficial layer cells with wide receptive fields in area 17.

Further processing of noise sensitivity in area 17 could occur via the strong reciprocal connections between layers III and V. Cells in layer Va have recurrent projections to the superficial layers (Lund et al. 1979; Gilbert and Wiesel, 1979; Martin and Whitteridge, 1984), which in turn project heavily to layer V (Creutzfeldt et al., 1977; Henry et al., 1978b; Lund et al. 1979; Gilbert and Wiesel, 1979, 1981a, 1983; Martin and Whitteridge, 1984). Moreover, Gilbert and Wiesel (1983) and Martin and Whitteridge (1984) have described complex or C-cells with such ascending and descending projections, and there is evidence that the collateral projection from the superficial layers excites C-cells in layer V. Thus, axon collaterals of layer III pyramidal cells make type I (presumed excitatory) synapses in layer V (Kisvarday et al., 1986), and antidromic stimulation of cortico-cortical efferents of layer III cells produces short-latency EPSPs in some layer V complex cells (Ferster and Lindstrom, 1983). In addition to these interlaminar projections, pyramidal cells in layers III and V have axonal arborizations in their laminae of origin (Lund et al., 1979; Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984) where they make type I contacts predominantly with other pyramidal cells (Anderson et al., 1985; Kisvarday et al., 1986; Gabbott et al., 1987). Notably, a giant pyramidal (Meynert) cell in layer V of area 17 with strong binocular drive

and a large C-type receptive field has been shown to make abundant contacts with other Meynert cells in the same layer (Anderson et al., 1985; Gabbott et al., 1987). Thus, there is ample scope for the processing of noise sensitivity via circuits that do not involve S-cells, though C-cells may indeed receive some component of their excitatory drive from S-cells. In particular, C-cells may be the recipients of the projection to the superficial layers from layer IV spiny stellate cells and star pyramids (Lund et al., 1979; Gilbert and Wiesel, 1979, 1983; Peters and Regidor, 1981; Martin and Whitteridge, 1984c) which have S-type receptive fields (Kelly and van Essen, 1974; Lin et al., 1979; Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984). Indeed, there is now physiological evidence for such a projection (Ferster and Lindstrom, 1983, 1985).

As in area 17, some C-cells in area 18 receive a monosynaptic input from the thalamus (Tretter et al., 1975; Harvey, 1980a). Since Y-afferents provide the predominant thalamic input to area 18, they must also be responsible for the major noise-sensitive pathway to Group I C-cells in this area, although a contribution from the W-cell input to area 18 (Hollander and Vanegas, 1977; Ferster and LeVay, 1978; Leventhal and Keens, 1978; Geisert, 1980; Meyer and Albus, 1981b) can not be excluded. The vast majority of C-cells in the infragranular layers, and all layer V cortico-tectal cells, are indirectly-driven by thalamic afferents (Harvey, 1980a,b). These cells presumably receive their noise-sensitive input predominantly from directly-driven C-cells in layers IIIb and IVa (Harvey, 1980a) which could also supply indirectly-driven C-cells in the superficial layers. Monosynaptically excited Group I C-cells in the superficial layers may be the border pyramids whose basal dendrites extend into layer IV and make contact with Y afferents (Freund et al., 1985b), or the large pyramidal cells prevalent some 200μm above the border with layer IV (Humphrey et al., 1985b) which could receive a direct input from Y-afferents whose arborizations extend some 200-400μm into layer III (Freund et al., 1985a; Humphrey et al., 1985b).

There is good reason to suspect that areas 17 and 18 receive noise-sensitive input

via the strong reciprocal connections between the two areas. These projections arise predominantly from the supragranular layers, but also from the deep layers, and involve some of the large pyramidal cells in layers III and V (Gilbert and Kelly, 1975; Gilbert and Wiesel, 1981b; Meyer and Albus, 1981a; Symonds and Rosenquist, 1984b; Bullier et al., 1984b; Martin and Whitteridge, 1984). Indeed, it has been claimed that the projection from area 17 to area 18 derives predominantly from C- and B-cells (Bullier et al., 1984c). Cells projecting to area 18 from the superficial layers of area 17 are concentrated in layer III and the III/IV border region (Gilbert and Wiesel, 1981b; Bullier et al., 1984b) where strongly noise-sensitive cells are found (Hammond and Smith, 1983, 1984). Since some superficial-layer cells in area 17 with cortico-cortical efferents also project to layer V (Gilbert and Wiesel, 1981a; Ferster and Lindstrom, 1983), it is conceivable that the same Group I C-cell in layer III of area 17 provides noise-sensitive input to the infragranular layers and to area 18. Area 18 cells projecting to area 17 are found throughout the superficial layers, although there is a slight sparing of the layer III/IV border region (Bullier et al., 1984b). It may be significant that in the superficial layers of area 18, large pyramidal cells are prevalent some 200μm above this border (Humphrey et al., 1985b).

Connections between the infragranular layers of areas 17 and 18 are restricted largely to layer V (Bullier et al., 1984b), where C-cells are predominant (Leventhal and Hirsch, 1978; Henry et al., 1979; Bullier and Henry, 1979c; Harvey, 1980a; Orban and Kennedy, 1981; Martin and Whitteridge, 1984). There is some evidence that the projection from layer V arises via axon collaterals of subcortically-projecting cells (Meyer and Albus, 1981a; Martin and Whitteridge, 1984), and layer V cells which project to the pons (Gibson et al., 1978) or to the NOT (Schoppmann, 1981) respond vigorously to motion of random patterns. Cells in areas 17 and 18 which project to the superior colliculus or to the pulvinar are large pyramidal cells in layer V (Gilbert and Kelly, 1975; Mason, 1978; Lund et al., 1979), which are also probably strongly noise-sensitive (see below). Indeed, Mason (1981) found good noise sensitivity in fibre recordings from both these

areas, and there is evidence for substantial branching in subcortical projections to pre-oculomotor structures (Albus and Donate-Oliver, 1977; Lund et al., 1979; Schoppmann, 1981; Baker et al., 1983). Moreover, some subcortically-projecting C-cells in layer VB, including giant pyramidal cells, have been shown to innervate the infragranular layers of area 18 (Martin and Whitteridge, 1984; Martin, 1984). Finally, further processing of noise sensitivity potentially occurs via the reciprocal connections of areas 17 and 18 with the cortico-recipient zone (CRZ) of the pulvinar (Kawamura et al., 1974; Updyke, 1977; Graybiel and Berson, 1980; Miller et al., 1980), which contains cells which respond strongly to noise (Mason, 1981). Significantly, afferents from the CRZ of the pulvinar arrive in layer I and at the layer IV/V border region in area 17 and, in addition, in upper layer III in area 18 (Miller et al., 1980), and thus could provide noise-sensitive input to Group I C-cells. Cells in the RRZ of the pulvinar, however, together with those in the dLGN and MIN, give a weak response to moving noise which is related to the individual elements in the noise sample (Mason, 1979a,b; 1981), indicating that good noise sensitivity is established first at the level of the visual cortex. In the superior colliculus, strongly noise-sensitive cells are recorded in the vicinity of the cortico-tectal input, but ventral to the retino-collicular termination zone (Mason, 1979). Moreover, following ablation of areas 17, 18 and 19, a greater proportion of collicular units are preferentially responsive to the 'structure' in the noise sample rather than to motion of noise per se (Mason, 1979).

The strong noise sensitivity of layer V cells in areas 17 and 18 is presumably important for the projection to pre-oculomotor structures such as the NOT (Schoppmann, 1981), which is involved in optokinetic nystagmus (Hoffmann, 1982), and the superior colliculus (Hollander, 1974; Palmer and Rosenquist, 1974; Gilbert and Kelly, 1975; Magalhães-Castro et al., 1975; Harvey, 1980b), which controls co-ordinated eye movements necessary for orientation in space. In this context it is noteworthy that the responses of cells in the superior colliculus fulfil all the prerequisites for a distinction between self-movement and movement of an object (Fromel, 1980a,b). Finally, the projection to the pons (Albus and Donate-

Oliver, 1977; Kawamura and Chiba, 1979; Albus et al., 1981) may be important for monitoring the movement of the animal with respect to the terrain, and thus contribute to visual guidance of movements (Gibson et al., 1978).

8.2. DIRECTIONAL TUNING OF CELLS IN AREA 17 AND AREA 18

In the present section the results described in Chapter 6 are discussed, in which directional tuning of cells in areas 17 and 18 was compared for motion of visual noise, bar and single spot stimuli.

8.2.1. Influence Of Velocity On Directional Tuning For Noise Motion

The present study provides the first quantitative comparisons of directional tuning in area 18 cells for noise and bar motion over a range of velocities, while comparable results in area 17 cells for the most part merely confirm those of previous work (Hammond and Reck, 1980b; Hammond and Smith, 1983). In both areas, preferred directions for noise and bar motion were dissimilar, and directional tuning for noise was labile and varied with velocity. Tuning for noise was typically unimodal at low velocity, but became progressively more bimodal as velocity was increased. With the exception of VHP cells in area 18, velocity bandpass was higher for noise than for bar motion. Gibson et al. (1978) mentioned that some area 18 cortico-pontine cells had dissimilar preferred directions for motion of a grating and a multiple spot stimulus. That differences in preferred directions for the two stimuli were not found in all cells is probably due to the coarseness of measurements of directional tuning (made at 45° intervals), together with a failure to appreciate the dependence of directional tuning for a random noise pattern on velocity. Schoppmann (1981), on the other hand, remarked that in layer V cells in areas 17 and 18 which project to the NOT, directional tuning for a random pattern was not dependent on velocity. Interestingly, however, these cells showed

sharp velocity tuning for noise, with preferred velocities ranging from 1-10 /sec. Area 18 cells in the present study preferred much higher velocities of noise motion, and none had an optimum velocity for noise within the range reported by Schoppmann (1981). The present results suggest that the velocity tuning for noise reported by Schoppmann (1981) reflects stimulation in the preferred direction for bar motion, whereas preferred and upper cut-off velocity for noise are much higher when measurements are made at the preferred direction at each velocity.

The velocity-dependent changes in directional tuning for noise were unrelated to amplitude of motion, which remained constant for different velocities. Nor could the lability in tuning for noise be attributed to changes in the waveform of stimulus motion with velocity. Stimulus motion was periodic at the lowest velocity tested, but aperiodic at all other velocities, with an increase in inter-sweep interval accompanying each increase in stimulus velocity (see Fig. 4.1). However, most cells showed progressive changes in the tuning profile for noise as velocity was increased over a wide range, whereas the differences in inter-sweep interval for different stimulus velocities were most pronounced at low velocities. Moreover, for all but the lowest three velocities tested, inter-sweep interval was well in excess of the 500ms necessary for demonstrating responses to high stimulus velocities in area 18 cells (Dinse and von Seelen, 1981a); it was precisely at these higher velocities, where inter-sweep interval remained relatively constant, that the most dramatic changes in tuning for noise were observed in some cells (Figs. 6.5*A-E* and 6.6*A-E*). Pertinently, velocity-dependent changes in directional tuning for noise, comparable to those reported here, have been demonstrated in area 17 complex cells, using periodic stimulus motion only (Hammond and Reck, 1980b; Hammond, 1981b; Hammond and Smith, 1983).

Movshon et al. (1980) speculate that bimodal tuning for noise at high velocities is an expression of a cell's sensitivity to the vectorial component of texture velocity in the preferred direction for a moving bar. Since the vector of velocity in the preferred direction for the bar is lower than the velocity of noise motion to

either side, this hypothesis predicts the higher cut-off velocity for noise than for bar motion. Orban (1984) argues that the similarity in the proportion of C-cells (some 30%) with bimodal tuning for noise (Hammond, 1978c) and VLP functions for bar motion (Orban et al., 1981a) supports Movshon et al.'s (1980) hypothesis. However, Hammond (1978c) made directional tuning comparisons at the optimal velocity for bar motion, at high velocity, most area 17 cells show bimodal tuning for noise (Hammond and Reck, 1980b; Hammond and Smith, 1983, present study). Moreover, as pointed out by Hammond and Smith (1983) and confirmed in the present study, the results from many cells in area 17 are inconsistent with Movshon et al.'s (1980) interpretation. Thus, some cells remain unimodally tuned at all velocities of noise motion to which they respond. When tuning for noise is bimodal with lobes of unequal strength, tuning for bar motion is commonly broader on the flank closest to the preferred direction for noise. Moreover, in the present study, some cells showed variations with velocity in tuning for bar motion which were associated with the velocity-dependent changes in tuning for noise (see section 8.2.2). Finally, bimodality of tuning can develop below the preferred velocity for bar and noise motion.

In the present study, VLP cells in area 17 and VBB cells in both areas could develop bimodal tuning below the preferred velocity for noise. VBB cells were bimodally tuned for noise at or below the preferred velocity for bar motion, though it was established for those in area 18 that bimodality was most pronounced at high velocities when the bar response was on the decline. For comparisons of directional tuning for noise over a range of velocities, the most interesting cells were VT and VHP cells in area 18, whose response to bar motion increased steeply with velocity over a wide range. According to the hypothesis of Movshon et al. (1980), all VT cells should show velocity-dependent modality of tuning for noise, but become bimodally tuned only at high velocity when the response to the bar is on the decline. VHP cells, on the other hand, should remain unimodally tuned at all velocities, with the same preferred directions for noise and bar motion. However, VT cells could develop bimodal tuning below the preferred velocity for

bar or noise motion, though the intervening trough was broader and deeper at high velocities when the response to both stimuli was on the decline. Some VHP cells showed velocity-dependent modality of tuning for noise, becoming progressively more bimodally tuned with velocity over a wide range, in parallel with a steep increase in response to bar and noise motion. Moreover, a high proportion of VT and VHP cells were strongly bimodally tuned for noise at the lowest velocity tested, well below the optimum for bar or noise motion. Indeed, one VHP cell had completely discrete lobes of tuning for noise below the threshold velocity for bar motion (Fig. 6.6K–O). A few VT and VHP cells did remain unimodally tuned for noise at all velocities, but these cells had radically dissimilar preferred directions for bar and noise motion below the preferred velocity for either stimulus. Orban and Callens (1977b) described an area 18 cell with a VHP function for motion of a slit, unimodal directional tuning for a random square pattern moving at high velocity and a VHP function for a random square pattern moving in the preferred direction for that stimulus. These observations are not inconsistent with the hypothesis of Movshon et al. (1980), though Orban and Callens (1977b) did not state explicitly that the direction of motion at which velocity-response functions were derived was the same for the slit and the random pattern. The present results demonstrate that VHP cells have comparable velocity-response functions for bar and noise motion only when measurements are made at the preferred direction for the two stimuli at each velocity.

A number of other observations on cells in both areas 17 and 18 were inconsistent with the hypothesis of Movshon et al. (1980). Thus, some cells were direction-selective for bar motion at all velocities but responded to noise moving in the non-preferred direction. Moreover, irrespective of direction sensitivity for bar motion, modality of tuning for noise could differ, at least at some velocities, for opposite directions of motion. Typically, in the preferred direction, unimodal tuning for noise gave way to bimodal tuning as velocity was increased, while in the non-preferred direction, tuning remained unimodal at all velocities. The single peak in the non-preferred direction was approximately 180° away from one of the peaks

which developed at high velocity for noise moving in the preferred direction. The presence or absence and magnitude of suppression of firing in the non-preferred (null) direction was velocity-dependent for both noise and bar motion, but the changes in magnitude of null-suppression frequently did not occur in parallel for the two stimuli. Finally, in asymmetrically tuned cells, the preferred direction for a spot shifted away from the preferred direction for a bar towards that for noise. Thus, at least in cells with asymmetrical tuning for bar motion, it was possible to demonstrate unequivocally that preferred direction is not invariant for all stimuli.

The present results, in conjunction with those from previous studies (Hammond and Reck, 1980b; Hammond and Smith, 1983) indicate that Movshon et al.'s (1980) hypothesis is inadequate to explain dissimilar directional tuning for bar and noise motion. It has been suggested (Hammond and Reck, 1980b; Hammond and Smith, 1983) that the trough between the two lobes of tuning for noise arises through inhibitory convergence from horizontally neighbouring cells with only slightly different preferred directions. Net excitation would then be most prominent at directions to either side of that preferred by the cell for a bar. Bimodally tuned cells would receive input from two groups of unimodally tuned cells, or from other cells with bimodal tuning. The intracortical, noise-sensitive input could arise not only from cells in the same or neighbouring columns, but also via horizontal excitatory connections between distant columns. Thus, superficial-layer pyramidal cells have long distance horizontal projections with axonal arborizations distributed in distinct clusters in layers III and V, which are in register radially (Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984; Kisvarday et al., 1986), the distance between clusters approximating the width of a hypercolumn (Gilbert and Wiesel, 1983). These horizontal collaterals make type I (presumed excitatory) contacts preferentially onto dendritic spines (Kisvarday et al., 1986), and thus may be responsible for the correlated firing of cell groups in different orientation 'columns' but with similar orientation preference (Ts'o et al., 1986). The notion of intercolumnar inhibitory convergence gains support from studies which have demonstrated that intracortical inhibition extends horizontally for distances

in the range 100-400μm (Hess et al., 1975; Toyama et al., 1981a,b), and that the inhibitory contribution to an area 17 complex cell's orientation selectivity is greatest to either side of its preferred orientation (Sillito, 1979). However, in comparable experiments to those performed by Sillito (1979), Vidyasagar and Heide (1980) found little effect of iontophoretic blockade of GABA-mediated inhibition on the orientation tuning of many area 18 cells. They suggested that the orientation specificity of area 18 cells is established by the excitatory input from area 17. This hypothesis is difficult to reconcile with the finding that orientation-selective cells are recorded in area 18 after acute lesions in area 17 (Dreher and Cottee, 1975), and that the orientation tuning of area 18 cells is unaltered by reversible cooling of area 17 (Sherk, 1978). After chronic lesions in area 17, Donaldson and Nash (1975b) found a slightly higher proportion of non-oriented cells in area 18. However, the major finding was a dramatic increase in the proportion of visually-unresponsive cells recorded postoperatively in area 18, which may at least partially reflect the retrograde degeneration during the long interval between surgery and the postoperative study of Y-fibres which branch and supply both areas 17 and 18 (Geisert, 1980; Bullier et al., 1984a; Freund et al., 1985a; Humphrey et al., 1985b; Birnbacher and Albus, 1987). Vidyasagar and Heide (1980) sampled only a few layer IV cells, and it may be that they recorded predominantly from second order units, which received an orientation-biased input from other area 18 cells. Moreover, the slight broadening of orientation tuning found in some area 18 complex cells during iontophoretic blockade of GABA-mediated inhibition is not unlike that seen in many area 17 complex cells (Sillito, 1979).

Matsubara et al. (1985, 1987a) have reported results that are at least consistent with the existence of laterally directed inhibitory connections in area 18. By comparing maps of orientation columns determined physiologically with the clustered distribution of label after focal extracellular HRP injections, they concluded that local interconnections exist between columns of almost orthogonal specificity and suggested that these were inhibitory. However, a large proportion of cells labelled by local application of HRP are pyramidal cells (Rockland and Lund, 1983;

Matsubara et al., 1987a), which are thought to be excitatory. At least in area 17, superficial- and deep-layer pyramidal cells with long-range tangential projections make contact predominantly with other pyramidal cells (Kisvarday et al., 1986; Gabbott et al., 1987). Thus, given the repeat interval of the axon collateral clusters of superficial-layer pyramidal cells in area 17 (Gilbert and Wiesel, 1983), and the correlated firing of distant cell groups with similar orientation preference in the same area, it is surprising that Matsubara et al. (1985, 1987a) did not observe excitatory connections between columns of like specificity in area 18.

Of the putative inhibitory interneurones in the visual cortex, large (multipolar) basket cells in layers III and V have axon collaterals in the appropriate range to account for the postulated laterally directed inhibitory interconnections which would produce bimodal tuning for noise and sharpen tuning for bar motion (Martin et al., 1983; Somogyi et al., 1983; Somogyi and Soltesz, 1986; Kisvarday et al., 1987). Their axons give rise to clusters of boutons, with a periodicity of 100-200μm, which can extend up a radial column of their target cells. Thus, since large basket cells make synapses preferentially on somata and proximal dendrites (Somogyi et al., 1983), they could provide inhibitory input to target neurones in different laminae but in the same orientation column. The largest pyramidal cells in layer III and giant pyramidal cells in layer V are among the favorite postsynaptic targets of large basket cells in area 17 (Somogyi et al., 1983; Kisvarday et al., 1987). Recent evidence suggests that area 18 may also contain large basket cells with long-range tangential projections. Matsubara et al. (1987b) have identified in layers III and V of area 18, large multipolar cells and long horizontally-directed fibres which are GABA-immunoreactive.

That tuning for noise becomes progressively more bimodal with increase in velocity may reflect an increase in the strength of the inhibitory input. It has been suggested (Hammond and Reck, 1980b; Hammond and Smith, 1983) that the trough separating the two lobes of tuning may arise through self-inhibitory feedback, preventing cell overload. Two observations in the present study, how-

ever, make this hypothesis less attractive. First, particularly in area 18, some cells were bimodally tuned at low velocity when response to noise was relatively weak. Secondly, in VHP cells with velocity-dependent modality of tuning, the trough separating the two lobes broadened and deepened with velocity while the response to bar motion continued to increase. Moreover, as pointed out by Hammond (1978c), in addition to activating the directional mechanism, motion of a noise field presumably influences the orientational mechanism according to the degree of non-coherence of individual elements across the cell's preferred orientation. At least in area 17, complex cells are relatively tolerant of luminance gradient reversal along the axis of optimum orientation (Hammond and MacKay, 1983a, 1985), and those in the deep layers respond preferentially to widely spread arrays of short line elements of common orientation rather than to single lines of preferred orientation (Hammond and MacKay, 1977). Thus, directional tuning for noise motion at a given velocity probably reflects the genuine directional input to a cell and the extent to which visual noise is capable of stimulating the orientational mechanism. In this context there was some indication that the degree of bimodality in tuning for noise at a given velocity was associated with strength of response to bar motion. Thus, among cells with velocity-dependent modality of tuning, VLP cells became strongly bimodally tuned at lower velocities than VBB or VT cells, while VHP cells developed bimodal tuning at higher velocities than other cells. Among VBB cells, those in area 18 tended to become strongly bimodally tuned at higher velocities than those in area 17, and this difference seemed to be associated with the relatively wider range of preferred velocities of VBB cells in area 18. Further, a high proportion of VT and VHP cells (which responded relatively weakly to bar motion at low velocity) were bimodally tuned for noise at all velocities, while in cells which remained unimodally tuned at all velocities, tuning for noise and bar motion at low velocity was more radically dissimilar in VT and VHP cells than in VLP and VBB cells. In VT and VHP cells which remained either unimodally or bimodally tuned at all velocities, the relative response to noise moving in the preferred direction for the bar could increase with velocity in parallel with the increase in response to bar motion. In the

absence of a response to bar motion (at velocities below threshold or above upper cut-off), cells either had two discrete lobes of tuning for noise or a single preferred direction which was radically different from that for the bar. This latter observation suggests that the tuning of the directional and orientational mechanisms may be radically dissimilar at all velocities, but that this difference is blurred at some velocities by the excitation of the orientational mechanism by moving noise. This would partially account for Orban and Callens' (1977b) finding of unimodal directional tuning for a random square pattern moving at high velocity and comparable velocity-response functions for slit and random pattern motion in a VHP cell in area 18: motion of a random *square* pattern presumably provides greater drive to the orientation mechanism than the pseudo-random visual noise used in the present study. On the other hand, it seems necessary to postulate an increase in the gain of the inhibitory input with velocity. Even in cells with pronounced bimodality of tuning for noise at low velocity, the intervening trough broadened as velocity was increased, causing the two peaks to become more disparate, while in cells with velocity-dependent modality of tuning, the trough which developed at high velocity was, in exceptional cases, wider than the total bar tuning width (see also Hammond and Reck, 1980b).

8.2.2. Directional Tuning Comparisons For Motion Of Noise, Bar And Spot Stimuli

Much as moving noise presumably influences the orientation mechanism, a moving bar must provide some drive to the directional mechanism. In this context it is noteworthy that almost one half of noise-sensitive cells in areas 17 and 18 had broader tuning for bar motion on the flank closest to the preferred direction for noise. This result is consistent with the similarly high incidence of asymmetrically tuned cells in areas 17 and 18 reported by Hammond and Andrews (1978), and demonstrates that the relationship in asymmetrically tuned cells between tuning profile for bar and noise motion, which was originally described in area 17

(Hammond, 1978c), also obtains in area 18. Moreover, at velocities for which the preferred directions for bar and noise motion were radically dissimilar, the preferred direction for a moving spot, which presumably provides relatively stronger drive to the directional mechanism than a moving bar, shifted towards the preferred direction for noise. A similar shift in preferred direction for spot motion was found by Bishop et al. (1968) in an area 17 hypercomplex cell, asymmetrically tuned for bar motion and bimodally tuned for noise with lobes of unequal strength. The finding of dissimilar preferred directions for bar and spot motion in a high proportion of noise-sensitive cells in areas 17 and 18 seems at variance with the results of Henry et al. (1974b), who reported that in area 17 complex cells, the only effect of reducing the length of a moving bar is to broaden directional tuning. However, this conclusion is based on data from only 5 cells, the illustrated example having rather symmetrical tuning for motion of a long bar, and Henry et al. (1974b) used only elongated stimuli. In the present study, it was established that symmetrically tuned cells have comparable preferred directions for bar and spot motion, while asymmetrically tuned cells have similar preferred directions for motion of a long and a short bar.

As suggested by Hammond (1978c), in noise-sensitive, asymmetrically tuned cells tuning may be sharper and more symmetrical for a stationary oriented stimulus. There is some evidence for this [P. Hammond and D. P. Andrews, unpublished observations (see Hammond, 1978c), Bishop et al., 1968, and Heggelund and Moors (1983) mention that orientation tuning was broader for moving than for stationary slits in some area 17 cells]. A number of observations in the present study were consistent with the notion that in asymmetrically tuned cells broadness of tuning for bar motion was associated with noise sensitivity. First, noise-sensitive asymmetrically tuned cells were found mainly in Group I, where they were predominant among cells with velocity-invariant bar tuning. Secondly, among asymmetrically tuned C-cells, those sensitive to noise were more broadly and more asymmetrically tuned than those insensitive to noise. Thirdly, among noise-sensitive C-cells, those with asymmetrical bar tuning were more broadly tuned than those with symmet-

rical bar tuning, while noise-insensitive symmetrically and asymmetrically tuned cells did not differ substantially in broadness of tuning. Fourthly, in asymmetrically tuned cells which were direction-selective for noise but gave more than a negligible response to bar motion in the non-preferred direction, bar tuning was narrower and more symmetrical in the non-preferred than in the preferred direction. Such differences in tuning width were seen only in noise-sensitive, asymmetrically tuned cells. bidirectional or direction-biased cells, asymmetrically tuned for bar motion but noise-insensitive, had comparably broad and asymmetrical tuning for opposite directions of bar motion. Finally, in asymmetrically tuned cells, suppression of spontaneous activity was occasionally observed on the sharper of the two flanks of bar tuning, or over a greater range of directions on this flank. In such cases the response to noise moving in directions corresponding to the suppression in the bar tuning curve was relatively weak or absent.

Some 25% of noise-sensitive cells in areas 17 and 18 showed variations in tuning for bar motion which were associated with the velocity-dependent changes in tuning for noise. In all cells with labile tuning for bar motion, bar tuning was broader at high than at low velocities. Some cells showed a reversal in the direction of asymmetry in tuning for bar motion as velocity was increased, which was related to the velocity-dependent changes in the relative size of the two lobes in the bimodal tuning curve for noise. In the remaining cells, tuning became progressively more asymmetrical with increase in velocity, or was symmetrical at low and markedly asymmetrical at high velocities. Significantly, in such cases response to noise increased steeply with velocity, and broadening of bar tuning occurred primarily on the flank closest to the major lobe of tuning for noise which developed at high velocities. Exceptionally, the preferred direction for bar motion shifted at high velocity towards the preferred direction for noise. A plausible explanation for lability of tuning for bar motion is that the degree to which a moving bar excites the directional mechanism varies with the magnitude of the directional input to a cell, as indicated by the response to noise moving in directions to either side of that preferred for a bar. That cells with labile bar tuning were found only among

Group I C-cells is consistent with this interpretation. The few cells which showed a dramatic increase with velocity in response to noise, but had velocity-invariant bar tuning were chiefly symmetrically tuned cells, in which stimulation of the directional mechanism by a moving bar may not cause a suprathreshold response (see below).

The finding of labile tuning for bar motion in a significant proportion of noise-sensitive cells seems somewhat controversial in view of reports that in area 17 complex cells, preferred direction and sharpness of bar tuning are velocity invariant (Hammond and Reck, 1980b; Hammond and Smith, 1983). However, lability of bar tuning was not artefactual. Broadening of bar tuning could not be ascribed to deepening of anaesthesia (Ikeda and Wright, 1974) or to deterioration of the preparation while, contrary to reports of fluctuations in optimal orientation (Horn and Hill, 1969; Donaldson and Nash, 1975a), directional tuning for an oriented stimulus in areas 17 and 18 is invariant with time (Hammond et al., 1975; Hammond and Andrews, 1978). As with the velocity-dependent changes in directional tuning for noise, lability of tuning for bar motion was not attributable to the differences in inter-sweep interval at different stimulus velocities. In cells with labile tuning for bar motion, tuning became progressively broader as velocity was increased over a wide range, and in some cases the most dramatic changes in bar tuning occurred at relatively high velocities where the changes in inter-sweep interval were comparatively small (Figs. 6.6*A–E* and 6.8*E–I*). Using periodic stimulus motion at all velocities, Hammond (1981b) and Hammond and Smith (1983) have demonstrated velocity-dependent changes in tuning for bar motion in area 17 complex cells. Hammond (1981b) illustrates an area 17 complex cell whose bar tuning became progressively broader and more asymmetrical with velocity, in parallel with a dramatic increase in the response to noise moving in directions corresponding to the broader flank of bar tuning. Similarly, Hammond and Smith (1983) describe an area 17 complex cell whose bar tuning was symmetrical at low velocity, but showed a repeatable asymmetry at high velocity, with broader tuning on the flank closest to the major lobe in the bimodal tuning curve for noise. Lability of bar

tuning may, however, be more common in area 18 than in area 17. In the present study, cells with labile bar tuning comprised a higher proportion of Group I C-cells in area 18 than in area 17, although this difference was not statistically significant. Further, cells with labile bar tuning were relatively common among VHP and VT cells, which are rare in area 17 (Orban et al., 1981a). On the other hand, VHP cells formed only a small proportion of the present sample of noise-sensitive cells in area 18 while, according to Orban et al. (1981a), this cell type is associated with the C family and is predominant among area 18 cells with receptive fields more than 10° from the area centralis projection.

Noise-sensitive cells with labile or asymmetrical tuning for bar motion had the broadest bar tuning. Among noise-sensitive cells, 'labile' cells were found exclusively, 'asymmetrical' cells predominantly in Group I, and among C-cells, those in Group I had the broadest bar tuning. Thus, if the broad directional tuning in 'labile' and 'asymmetrical' cells reflects the stimulation by a moving bar of the directional mechanism, C-cells in different groups may not differ substantially in tuning for a stationary, flash presented oriented stimulus. On the other hand, it remains to be established that noise sensitivity is a prerequisite for differential tuning for moving and stationary bar stimuli. Heggelund and Moors (1983) report that tuning was broader for moving than for stationary slits in a sample of area 17 cells which included simple cells, while Hammond and Andrews (1978) found a high degree of asymmetry of tuning for bar motion in area 18 complex type 1 cells, which were equated with area 17 simple cells. Nevertheless, the finding that directional tuning for bar motion can vary with velocity confirms that it does not merely reflect orientation tuning.

If in cells with asymmetrical or labile bar tuning a moving bar is capable of stimulating the directional mechanism, why do some noise-sensitive cells remain symmetrically tuned for bar motion even for velocities at which tuning for noise is bimodal with lobes of unequal strength? Cells with symmetrical tuning for bar motion had conspicuously narrow bar tuning, and those which were spontaneously

active showed suppression of firing on both sides of the excitatory profile for the bar. The magnitude of suppression declined with velocity in parallel with an increase in response to noise moving in directions corresponding to the suppression in the bar tuning curve. Thus, to be speculative, a bar moving in directions to either side of the excitatory tuning profile may provide some drive to the directional mechanism, but simultaneously evoke powerful orientation-sensitive inhibition which prevents the response reaching threshold. In this context, it is noteworthy that among symmetrically tuned C-cells, there was no difference in broadness of tuning between those sensitive and those insensitive to noise. Further, unlike noise-sensitive cells with asymmetrical bar tuning, noise-sensitive, symmetrically tuned cells had comparably broad and symmetrical tuning for opposite directions of motion, irrespective of direction sensitivity for noise. Thus noise-sensitive, symmetrically tuned cells may have similar tuning for stationary and moving oriented stimuli.

8.2.3. Directional Tuning For Bar Motion Of Different Cell Types In Area 18

The present study provides the first quantitative comparisons of directional tuning for bar motion of C-, S-, B- and A-cells in area 18. C-cells had the broadest, S- and B-cells the narrowest tuning. C-cells were significantly more broadly tuned than S- or B-cells, while the directional tuning of the few A-cells recorded did not differ strikingly from that of C-cells. C-cells in areas 17 and 18 had comparably broad directional tuning. These results are in good agreement with the directional tuning of C-, S-, B- and A-cells determined qualitatively by Orban and Kennedy (1981) (and see Orban, 1984). The only previous quantitative study of directional tuning in area 18 is that of Hammond and Andrews (1978), who used a rather different cell classification scheme. Their values for average half-width of tuning for complex cells in areas 17 and 18 are comparable to, if slightly higher than, those reported here for C-cells in the two areas. In contrast to the present finding

of a difference in tuning between area 18 C- and S-cells. Hammond and Andrews (1978) reported that area 18 complex cells were not substantially more broadly tuned than complex type 1 cells (equated with area 17 simple cells). However, since cell classification was based on responses to stationary, flashed-presented stimuli alone, the complex type 1 population probably included A-cells, and this may partially account for their broader tuning compared with area 18 S-cells in the present study. Nevertheless, the present finding that area 18 S-cells were more broadly tuned than their area 17 counterparts is consistent with the difference reported by Hammond and Andrews (1978) between area 18 complex type 1 cells and simple cells in area 17. The present values for broadness of tuning in the small sample of area 17 S-cells are comparable with those of Hammond and Andrews (1978) and of others for area 17 simple cells (Henry et al., 1973; Watkins and Berkley, 1974; Heggelund and Albus, 1978; Kato et al., 1978; Leventhal and Hirsch, 1978).

8.3. MODULATORY INFLUENCE OF MOVING VISUAL NOISE BACKGROUNDS ON RESPONSES OF AREA 18 CELLS TO MOVING ORIENTED STIMULI

8.3.1. Comparisons With Previous Results From Area 17

In Chapter 7, results were presented on the modulatory influence of moving background noise on the responses of cells in area 18 to an optimally-oriented, moving foreground stimulus. Bar and noise stimuli were swept synchronously in phase at the same velocity, and in both directions orthogonal to bar orientation. Background motion suppressed bar responses in all noise-insensitive cells in area 18 (classified on the basis of their lack of response to noise motion alone), but the magnitude of in-phase suppression was critically dependent on the length of the comparison bar. Percent suppression declined progressively with increasing bar

length presumably because, as it was lengthened, the bar obliterated an increasing amount of the noise background, thus providing progressive relief from the suppressive influence of moving noise.

The present results for area 18 S-cells can be compared with the modulation of simple-cell bar responses by background texture motion reported by Hammond and MacKay (1981b). In-phase motion of a background field of visual noise was suppressive of bar response in 74% of area 17 simple cells, and often caused total abolition of response (Hammond and MacKay, 1981b), whereas in the present study, only 55% of area 18 S-cells showed significant suppression of response to bars of optimal length, and the magnitude of suppression ranged from 14–95%. However, these differences in susceptibility to the suppressive influences of background motion may not as great as they seem. Hammond and MacKay (1981b) report that of the simple cells in which background motion was suppressive of bar response, many showed relatively weak suppression by moving noise backgrounds, and that stronger effects could be elicited by making texture velocity greater than bar velocity, or by using a checkerboard pattern rather than visual noise. In the present study, only visual noise was used as a background, and its velocity was always the same as that of the moving bar. Moreover, Hammond and MacKay (1981b) mention briefly that the magnitude of response suppression could be increased by using shorter comparison bars to yield relatively weak, criterion responses. This is in line with the present results for all noise-insensitive cells in area 18, though in a few C-cells with restricted length summation it was possible to demonstrate that the magnitude of suppression exerted by background motion was not related to the strength of the criterion response (which remained relatively constant), but was specifically dependent on the length of the bar used to obtain a criterion response.

In area 18, in-phase suppression by moving noise backgrounds was not restricted to cells in the S family, but could be demonstrated in all cells which were not driven by noise motion alone, by systematically varying the length of the comparison bar

A few superficial-layer complex and B-cells recorded in area 17 by Hammond and Smith (1984) were rather insensitive to noise motion alone, but showed suppression of bar-evoked responses by a synchronously moving noise background. In other superficial-layer complex cells, however, noise motion evoked negligible responses and was similarly uninfluential on responses to bar motion. These cells may nevertheless have received a potentially suppressive noise-sensitive input since, in the present study, conventional stimulation with a long bar showed many cells to be rather indifferent to synchronously moving noise backgrounds, yet reducing bar length revealed powerful suppressive influence of background motion on cell responsiveness.

The strong dependence of suppression on bar length may seem surprising given that, during simultaneous motion of bar and background, texture is obscured only along the axis of the bar and not in comparable locations to either side. However, at least in area 17 simple cells, the suppressive influence of synchronous background motion is weighted in favour of the receptive field centre, but is more extensive lengthwise than widthwise across the receptive field (Hammond and MacKay, 1981b). Thus, during in-phase motion, a bar moving over the most sensitive part of the receptive field, would simultaneously obliterate those texture elements responsible for the greatest amount of suppression. A further point is that, particularly for C- and A-cells, the use of peak firing frequency may have enhanced the dependence of suppression on bar length. Although these cells give a sustained response to a moving bar extending over the entire discharge region, there is an obvious peak in the histogram profile. Thus, stimulation of the receptive field centre by moving noise might be expected to exert powerful suppression of the response to a bar moving simultaneously over the least sensitive part of the receptive field, but this would have little effect on peak firing frequency. Indeed in many cells, synchronous background motion had little influence on the peak response to a long bar, but led to a sharper bar response profile.

The decline in percent suppression was non-linear, becoming progressively flatter

in slope as bar length was increased until an asymptotic value was reached. This observation is consistent with a decline in the potency of the suppressive influence of background motion with increasing distance from the centre of the receptive field along its axis, as has been reported for area 17 simple cells (Hammond and MacKay, 1981b). It should be emphasized, however, that in many cells requiring appreciable length summation for effective drive, longer starting lengths for the comparison bar resulted in less potent suppressive effects and less marked non-linearity of the function relating relative response to the combination stimulus and bar length.

While the non linear decline in percent suppression as a function of bar length was a consistent feature of the present results, the data from many cells allowed complementary or alternative interpretations. Thus, for cells in which the length-response functions for the bar and the combination stimulus had parallel ascending slopes, the possibility that the synchronously moving noise background depressed response by a fixed amount irrespective of bar length could not be excluded. However in some of these cells, background motion could be strongly suppressive of response to short bars, but have little or no influence on response to long bars, indicating that magnitude of response suppression was indeed dependent on the length of the comparison bar. For other cells in which the slope of length summation was steeper for the combination stimulus than for the bar (Fig. 7.2A), response *reduction* declined *linearly* with increasing bar length. However, the present results suggest that the inhibitory action of synchronously moving noise backgrounds is divisive rather than subtractive (see section 8.3.3.). Moreover in cells with very localized length summation, it was possible to demonstrate that both percent suppression and response reduction declined non linearly with bar length. Indeed, a non linear decline in percent suppression with bar length was found in all cells, irrespective of the relationship between the slopes of length summation for the bar and the combination stimulus. In cells with rather steep ascending slopes of length summation for the bar (Fig. 7.2C), the rising phase for the combination stimulus tended to be relatively flatter in slope. Thus with

increase in bar length, response reduction *increased* while percent suppression *decreased*. Further, cells in which the ascending slope of length summation for a bar was non-linear (Fig. 7.2E) showed neither a depression of response by a fixed amount irrespective of bar length, nor a linear decline in response reduction.

In end-free cells, the non-linear decline in percent suppression with bar length could be more protracted than the maximum estimate of receptive field length (extent of length summation or minimum response field length), suggesting that texture elements lying beyond the height of the conventional receptive field were capable of modulating response. Pertinently, Hammond and MacKay (1981b) found that in area 17 simple cells, the zone of background suppression could extend lengthwise beyond the borders of the excitatory receptive field. By contrast, in noise-sensitive complex cells, the influence of background motion on responses to foreground bar stimuli is restricted to the mapped receptive field (Hammond and MacKay, 1981b; Hammond and Smith, 1984). The present results suggest that the lengthwise extent of modulatory textural influences is related not to cell class, but to noise sensitivity. Thus, while texture drive to noise-sensitive cells is confined largely to the excitatory receptive field, the lengthwise extent of suppressive texture influences on noise-insensitive cells of all classes would not seem to be strictly related to receptive field length. Moreover, percent suppression of bar-evoked responses by synchronously moving noise backgrounds declined over a comparable range for opposite directions of motion, even when the extent of length summation was radically different in the two directions. Thus, suppressive textural influences may extend lengthwise over an area which is comparable for opposite directions of motion, but relatively independent of length summation characteristics in each direction.

No cell showed the significant enhancement of response to long bars observed by Hammond and MacKay (1981b) in some area 17 simple cells. However, this negative finding does not necessarily reflect an areal difference in sensitivity to noise backgrounds, since Hammond and MacKay (1981b) reported response facilitation

by whole-field texture motion in a mere 4% of simple cells, and the present sample contained only 14 S-cells.

8.3.2. Relation To End-Inhibition And Length Summation

Hammond and MacKay (1981b) reported that in the same *end-free* simple cells, whole-field texture motion was suppressive of bar response, while a patch of moving texture located outside the receptive field along its axis caused response facilitation. Thus, the suppressive influences of background motion in area 17 simple cells are distinct from end-inhibition. The same independence of response suppression by synchronously moving noise backgrounds and end-inhibition was also observed in area 18, for end-free cells of all classes were subject to powerful suppressive influences of background motion. Hammond and Smith (1984) attributed the suppressive influence of moving noise backgrounds on the responses of some area 17 complex cells to the presence of end-inhibition. However, at least in area 18, the apparently greater susceptibility of end-stopped cells to the suppressive influence of moving noise backgrounds reflects their preference for short bars: for the magnitude of suppression declined with bar length in all cells, irrespective of their length summation characteristics. Moreover, the present results argue strongly that in end-stopped cells, the mechanisms responsible for end-zone inhibition and response suppression by synchronous background motion are independent. First, the range over which percent suppression declined with bar length was unrelated to the length of the inhibitory end-zones, suggesting that the lengthwise extent of end-zone inhibition and of the suppressive influence of synchronous background motion could differ in the same cell. Secondly, in cells with direction-selective end-zone inhibition, synchronous motion of the noise background suppressed bar responses in both preferred and opposite directions. Thirdly, in the same end-stopped cells, percent suppression exerted by synchronous motion of the noise background was essentially invariant with velocity, while percent end-zone inhibition was velocity-dependent, being maximal at or near the preferred velocity for a

bar of optimal length. Finally, the magnitude of end-zone inhibition and response suppression by synchronous background motion could be radically different in the same cell. Pertinently noise-sensitive cells, which probably mediate suppressive textural influences (see below), may show end-inhibition when tested with moving bars, but not in response to moving texture (Hammond and Shorrocks, 1987)

Much as the suppression of bar-evoked responses by synchronously moving noise backgrounds was distinct from end-zone inhibition, the enhancement of bar response by synchronous background motion in Group I C-cells was independent of length summation characteristics for a bar. Thus, even cells with restricted length summation showed substantial facilitation of response to a spot or short bar. Pertinently, Hammond and Shorrocks (1987) found that area 17 cells with restricted length summation for bar motion could show substantial length summation when tested with moving texture. Thus, noise-sensitive cells would seem to receive separate bar and noise excitatory inputs — a conclusion which is supported by the present finding of differential short-term variability in the responsiveness of the same cell to noise and bar motion. The influence of background motion on responses to long bars was weak or negligible, and much less than predicted from an additive combination of responses to bar and noise motion alone. These results are complementary to those of Hammond and Smith (1983, 1984) who concluded that in area 17 complex cells an oriented stimulus in motion induces potent blockade of response to moving noise backgrounds. Investigation of the magnitude of response enhancement over a range of stimulus velocities demonstrated a further example of non-linear interaction between responses to bar and noise motion. Percent enhancement was not necessarily maximal at the preferred velocity for noise motion alone, but at a given velocity, seemed to depend on the relative strength of the separate responses to bar and noise motion.

8.3.3. Possible Mechanisms

As discussed in section 8.1.3, all specific afferents to visual cortex are thought to be excitatory (Gray, 1959; Eccles, 1964; Uchizono, 1965; Colonnier, 1968; Creutzfeldt and Ito, 1968; Garey, 1971; Garey and Powell, 1971; Toyama et al., 1974; Peters et al., 1976; Ferster and Lindstrom, 1983, but see Einstein et al., 1987). Thus, the suppressive textural influences on bar responses of area 18 cells would seem to be due to reduced excitatory drive from thalamic afferents and/or to an intracortical noise-sensitive inhibitory input. Gulyás et al. (1987) have recently claimed that cells in the dLGN and area 17 show comparably strong suppression of bar-evoked responses by synchronously moving noise backgrounds, and they concluded that the suppression of bar-evoked responses in area 17 is largely a reflection of that present in the geniculate input. This conclusion rests on the assumption that the separate responses to bar and noise motion add linearly for in assessing the modulatory influence of synchronously moving noise backgrounds. Gulyás et al. (1987) first subtracted the response to noise motion alone from the response to the combination stimulus, and compared the resultant response with that evoked by bar motion alone. Indeed, for cortical cells whose response to noise motion is independent of the 'structure' in the noise sample, the *demonstration* of response suppression depends on the assumption of linear additivity. However, the present results in area 18, together with those of previous studies in area 17 (Hammond, 1978c, 1981b; Hammond and Reck, 1980b; Hammond and Smith, 1983; Hammond and Shortocks, 1987) imply that excitatory noise and bar inputs are mediated by separate pathways, possibly acting at different sites in the same noise-sensitive cell. Contrary to the assumption of linear additivity and the hypothesis that background motion is suppressive of bar-evoked responses, there is evidence that in noise-sensitive cells the pathway mediating bar sensitivity *gates* that mediating noise sensitivity (Hammond and Smith, 1983; Hammond et al., 1986).

In cortical cells which give weak responses to motion of visual noise related to

certain larger-than-average grains in the noise sample, the demonstration of response suppression by synchronously moving noise backgrounds is independent of the assumption of linear additivity, both in area 17 (Hammond and Smith, 1984; Gulyás et al., 1987) and in area 18 (present study). This assumption is more critical, however, for an assessment of the modulatory influence of synchronous background motion on the bar-evoked responses of cells in the thalamus, which give relatively strong 'grain responses' to noise motion alone (Mason, 1976a,b; 1981); when a bar is embedded in a field of visual noise and both stimuli are swept in-phase, the response of geniculate X- and Y-cells to the bar is barely detectable in the dominant response to the noise, even at high signal-to-noise ratios (Hoffmann et al., 1980). However, the response to the bar stands out clearly against the mean response to different samples of noise; it is masked but not attenuated in the in-phase condition. This result implies that, on the assumption of linear additivity, the suppression of the bar-evoked responses of geniculate cells by synchronously moving noise backgrounds is maximal when, in the in-phase condition, the same noise pattern is swept repetitively across the receptive field [as was the case in the study of Gulyás et al. (1987)], but is much weaker when the noise sample is changed from sweep-to-sweep. By contrast, in both noise-insensitive and strongly noise-sensitive cortical cells, the magnitude of response modulation measured on the assumption of linear additivity, would presumably be independent of the 'structure' in the noise sample from sweep-to-sweep. Pertinently, for both simple cells and strongly noise-sensitive complex cells in area 17, the signal-to-noise detection thresholds for a moving bar embedded in a synchronously moving noise field are the same irrespective of whether the bar has to be detected in the response to the noise profile or in the mean response to the noise (Hoffmann et al., 1980). Thus, even on the assumption of linear additivity, it is difficult to see how the suppression of the bar-evoked responses of cortical cells by synchronously moving noise backgrounds can simply reflect the suppression present in the geniculate input. On the other hand, Gulyás et al.'s (1987) comparisons of the suppressive influence of synchronously moving noise backgrounds in the dLGN and area 17

imply that, if one rejects the assumption of linear additivity, response suppression is stronger in noise-insensitive cortical cells than in geniculate cells. Thus, the suppressive influence of synchronously moving noise backgrounds on the bar-evoked responses of cortical cells must be due, at least in part, to intracortical mechanisms.

There is independent evidence for intracortical, noise-sensitive inhibition. For in-phase motion of bar and noise stimuli, the signal-to-noise detection thresholds of simple cells in area 17 are lower than those of geniculate cells, implying that an intracortical inhibitory input suppresses the response to noise present in the geniculate afferents (Hoffmann et al., 1980). Furthermore, it seems necessary to postulate a direction- (axial) selective noise-sensitive inhibitory input to explain some of the observations on the sensitivity of area 17 cells to relative motion between a bar and its noise background (Hammond et al., 1985; Orban et al., 1987) and, in at least one extrastriate visual area, magnitude of response suppression by synchronously moving noise backgrounds has been shown to depend on the direction of background motion (von Grunau and Frost, 1983). Finally, in one noise-unresponsive cell recorded in area 18, synchronous motion of a bar and its noise background in the non-preferred (null) direction suppressed spontaneous activity and, in noise-responsive cells in area 17, synchronously moving noise backgrounds can potentiate null suppression caused by bar motion (Hammond and Smith, 1984; Hammond et al., 1986). This implies that synchronously moving noise backgrounds are capable of providing a postsynaptic inhibitory input to cortical cells.

The above observations impute intracortical mechanisms in the suppression of the bar-evoked responses of cortical cells by synchronously moving noise backgrounds, but do not exclude the possibility that response suppression in the cortex partially reflects a reduction in the excitatory drive from thalamic afferents. If the bar-evoked responses of geniculate cells are significantly suppressed by synchronously moving noise backgrounds, it is unlikely that the suppression

is mediated by an inhibitory loop via noise-sensitive cells in the visual cortex, for the cortico-geniculate projection derives predominantly from S-cells (Dubin and Cleland 1977, Harvey, 1980b, Boyapati and Henry, 1987). Furthermore, the suppression of bar-evoked responses by synchronously moving noise backgrounds is distinct from the 'periphery' or 'shift' effects seen in the retina and dLGN. In both area 17 (Hammond and MacKay 1981b) and area 18 (present study), the suppressive influence of synchronously moving backgrounds is spatially much more localised than the long-ranging inhibitory 'shift-effect' in the dLGN (Fischer and Kruger 1974), while in the retina, the magnitude of response to whole-field noise motion alone is dependent on interactions spatially limited to the classically-defined receptive field (Ahmed and Hammond, 1983): motion of visual noise confined to the receptive field centre elicits a stronger response than whole-field noise motion, and moving noise confined to the receptive field surround either produces a response which is weak compared with that to stimulation of the centre or causes suppression of spontaneous activity. Thus, synchronously moving noise backgrounds conceivably cause suppression of bar-evoked responses in some geniculate cells due to the antagonistic interaction between receptive field centre and surround; the direction and magnitude of response modulation would depend to a large extent on the noise sensitivity of the receptive field surround. Mason (1976a,b) reported that in some 20% of cells in the thalamus *whole-field* noise motion caused suppression of spontaneous activity — a finding which is consistent with the evidence for an increase in surround potency at the geniculate level (Hubel and Wiesel 1961, Hammond, 1974, Maffei and Fiorentini 1973). In these cells, the inhibition caused by motion of the noise field alone would be manifest during simultaneous motion of a bar and its noise background, as a suppression of the suprathreshold response to the bar. If the suppression of the bar-evoked responses of geniculate cells by synchronously moving noise backgrounds is indeed related to the potency of the receptive field surround, one would expect it to be stronger in X-cells, which project almost exclusively to area 17, than in Y-cells, which provide the predominant input to area 18. Furthermore, as discussed in

the Introduction. Y-cells which project to area 18 may have on average weaker receptive field surrounds than those which project to area 17.

Thus, it is concluded that the suppressive effects of synchronously moving noise backgrounds on the responses of cells in area 18 reflect to a small extent a reduction in excitatory drive from thalamic afferents, but are due predominantly to intracortical inhibition. The most obvious candidates for providing such inhibition are the strongly noise-sensitive, Group I C-cells in the deep and superficial layers which, it was argued, are predominantly large pyramidal cells. Pyramidal cells are thought to be excitatory in function, but could exert disynaptic noise-sensitive inhibition via an interneurone. However, layer III/IV border pyramidal cells and giant pyramidal cells in layer V have been shown to make synaptic contact almost exclusively with other pyramidal cells (Anderson et al., 1985; Kisvárday et al., 1986; Gabbott et al., 1987). Moreover, since the available evidence suggests that putative inhibitory interneurones are not distinguishable physiologically from other cells (Gilbert and Wiesel, 1979; Martin et al., 1983; Somogyi et al., 1983; Kisvárday et al., 1986), one would expect those providing the noise-sensitive inhibitory input to be noise-sensitive.

Percent suppression by synchronously moving noise backgrounds was essentially invariant over a wide range of stimulus velocities and relatively constant for preferred and opposite directions of motion. This suggests that the inhibitory action of synchronous background motion is divisive rather than subtractive. It has been calculated (Blomfield, 1974) that for large inhibitory conductances, a division-like change in firing rate is produced by inhibitory synapses located at the soma, while those located on the distal dendrites produce a subtractive change in response. If it is assumed that the suppressive influences of in-phase background motion on responses to optimally-oriented moving bars are due to an axo-somatic inhibitory input from noise-sensitive cells then, in view of the dissimilar directional tuning for bar and noise motion, the inhibition must arise predominantly from neurones in orientation columns neighbouring those of their target cells. Of the puta-

tive inhibitory interneurones which provide perisomatic input to pyramidal cells, short-axon multipolar cells and small basket cells, whose axonal arborizations are confined largely within the territory of the dendritic tree (Lund et al., 1979; Peters and Regidor, 1981; DeFelipe and Farinas, 1992), would seem poor candidates for mediating such inhibition. However, the extensive tangential projections of deep- and superficial-layer, large basket cells and the periodicity of their bouton clusters (100-200μm) (Martin et al., 1983; Somogyi et al., 1983; Somogyi and Soltész, 1986; Kisvárday et al., 1987) make them ideally suited to a role in intercolumnar inhibition. Interestingly, Martin et al. (1983) have described a large basket cell in layer III of area 17 with response properties typical of Group 1 C-cells recorded in the present study, and the involvement of large basket cells in mediating noise-sensitive inhibition would be consistent with the suggestion that strongly noise-sensitive cells have large somata (Hammond and Smith, 1984; and see section 8.1.). Further, Group 1 C-cells were predominantly direction-selective, while percent response suppression by moving noise backgrounds was relatively constant for opposite directions of motion and, in addition, was essentially invariant over a wide range of velocities. These results imply that the noise-sensitive inhibitory input derives from a pool of cells. Pertinently, Somogyi et al. (1983) have estimated that there is substantial convergence of large basket cells onto a single pyramidal neurone. Conceivably, large basket cells could mediate the noise-sensitive inhibitory input which suppresses bar-evoked responses in noise-insensitive cells and contribute to the inhibitory convergence that produces bimodal tuning for noise in noise-sensitive cells.

In areas 17 and 18, thalamo-cortical inhibition is mediated via a disynaptic pathway of the feed-forward type, though some cells disynaptically excited from the thalamus receive trisynaptic inhibition (Creutzfeldt and Ito, 1968; Toyama et al., 1974; Ferster and Lindström, 1983). In area 18, the majority of S-cells are monosynaptically excited by thalamic afferents, while most C-cells are indirectly-driven (Harvey, 1980a). As discussed in section 8.1.4, at least some Group 1 C-cells are likely to be monosynaptically excited from the thalamus, and the extracellular

study by Harvey (1980a) may have underestimated the proportion of monosynaptically excited cells in area 18 since, at least in area 17, sizeable EPSPs do not always bring a cell to threshold (Ferster and Lindstrom, 1983). Directly-driven Group I C-cells could provide disynaptic noise-sensitive inhibition to other monosynaptically excited cells, including most S-cells. C-cells with restricted length summation, which in the present study were found almost exclusively in Group I, are more often indirectly-driven than other C-cells (Harvey, 1980a), while cortico-tectal cells, which have properties characteristic of deep-layer Group I C-cells, are all indirectly-driven (Harvey, 1980b). These indirectly-driven Group I C-cells could mediate the trisynaptic, noise-sensitive inhibitory input to other disynaptically excited cells. That inhibition arrives via longer pathways than excitation raises the question of the relative timing of the excitatory and inhibitory inputs since, to be effective, the noise-sensitive inhibitory input must pre-empt the effects of the excitatory bar input. This problem cannot be solved by assuming that the inhibitory interneurone receives thalamic input via afferents which are faster-conducting than those which drive the target cell, since most area 18 cells receive thalamic input via Y-afferents (Stone and Dreher, 1973; Tretter et al., 1975; Harvey, 1980a; Dreher et al., 1980). However, since the temporal variability of response latency of X- and Y-cells in the retina masks the differences in retino-cortical transmission time along X and Y pathways (Bolz et al., 1982), it is unlikely that the relative timing of excitatory and inhibitory pathways depends on differences in conduction velocity of the functional types of thalamic afferent (see also Martin, 1984). In any event, there is evidence that area 17 cells receive excitatory and inhibitory inputs via thalamic afferents of the same functional type (Ferster and Lindstrom, 1983). The critical factor would seem to be the balance of the temporal summation characteristics of the excitatory bar input and the noise-sensitive inhibitory input: the inhibition must become effective before the threshold for an action potential discharge is reached. In this context, the axons of large basket cells, which are thick and heavily myelinated (Somogyi et al., 1983), are probably relatively fast-conducting compared with other intracortical axons. Moreover, if the noise-sensitive inhibition were exerted directly by large basket

cells, this would reduce the number of synapses between source and ultimate target, and so make for more rapid inhibition.

Martin et al. (1983) and Kisvárday et al. (1985) described a small basket ('clutch') cell with a C-type receptive field in layer IV of area 17. Since it had axonal arborizations restricted largely to layer IV, and presumably made contact predominantly with simple cells, it was implicated as a possible source of noise-sensitive complex-to-simple cell inhibition. However, the properties of this cell (monocular drive, narrow directional tuning and lack of directional bias) are typical of noise-insensitive C-cells. Moreover, the clutch cell has a relatively restricted axonal arborisation, which makes it ill suited to a role in intercolumnar inhibition. Finally, the postulated noise-sensitive inhibitory input would seem to involve inhibition from a pool of cells, and C-cells are rare in layer IV. On the other hand, there is little morphological evidence of an inhibitory input to layer IV from cells in layers III and V. Most basket cells in the superficial and deep layers do have radial projections, but their axonal arborisations are both less profuse and less extensive in layer IV (Peters and Regidor, 1981; Martin et al., 1983; Somogyi et al., 1983; Somogyi and Soltesz, 1986; Kisvárday et al., 1987). One superficial layer large basket cell recovered by Martin et al. (1983) did have an axonal arborization in layer IV with a lateral spread of 500μm, but this cell had an S-type receptive field. Thus, for some S-cells in layer IV, suppression of bar-evoked responses by synchronously moving noise backgrounds may not depend exclusively on a noise-sensitive inhibitory input. In noise-unresponsive S-cells with zero spontaneous activity, motion of visual noise alone may cause potent inhibition which becomes evident in the in-phase condition when the moving bar causes sufficient excitation to drive cell response above threshold. As discussed in section 8.1.3, such inhibition could be mediated by circuits within layer IV and need not be noise-sensitive.

8.3.4. Implications And Conclusions

The presents results can be related to those of comparable studies in areas 17 and 18 in which a Gaussian noise field was superimposed on a contrast bar in order to simulate a signal detection task (Hoffmann and von Seelen 1978, Hoffmann et al 1980 Dinse and von Seelen 1981b). In area 17, simple cells detect a moving bar embedded in a stationary noise field at higher signal-to-noise ratios than complex cells while for in-phase motion of bar and noise the signal detection thresholds of simple cells are lower than those of complex cells (Hoffmann and von Seelen, 1978). The threshold signal-to-noise ratios of complex cells for in phase motion are (understandably) related to the strength of response to motion of visual noise alone; those of simple cells are lower than those of geniculate X- and Y-cells, and plausibly reflect a suppression of the response to moving noise by complex cells with high threshold signal-to-noise ratios for in phase motion (Hoffmann et al 1980). Indeed, the low detection thresholds of simple cells for in-phase motion of a bar and superimposed noise (Hoffmann and von Seelen, 1978), and the suppressive influences of background motion on simple-cell responses to foreground bars (Hammond and MacKay 1981b) are probably an expression of the same inhibitory input. In the present study, powerful suppression of bar-evoked responses by synchronous background motion was demonstrated in all noise-insensitive cells in area 18 by systematically varying bar length. It was argued that such suppression is due predominantly to an intracortical noise-sensitive inhibitory input from Group I C-cells. Thus one might expect that, as in area 17, the detection thresholds of S-cells (and other noise-insensitive cells) in area 18 for a moving bar would be lower if its superimposed background were moved in-phase. However, Dinse and von Seelen (1981b) reported that the detection thresholds of all classes of area 18 cell were comparable whether the superimposed noise field was stationary or moved in-phase, and concluded that this represents an important difference between areas 17 and 18. A crucial point, however, is that due to the inappropriate spatial frequency range of the noise process used in Dinse and von Seelen's (1981b) study, area 18 complex cells did not respond to noise motion

alone, and thus could not have provided the postulated noise-sensitive inhibitory input to S-cells (and other noise-insensitive cells). Thus, that the signal detection thresholds of area 18 S-cells were comparable for stationary or moving, superimposed noise (Dinse and von Seelen, 1981b) almost certainly reflects the absence of a noise-sensitive inhibitory input to suppress the response to moving noise in the in-phase condition. Conversely, had noise motion alone provided excitatory drive to C-cells, they would presumably have had higher detection thresholds for in-phase motion of a bar and superimposed noise.

Thus in the light of the present results, it seems reasonable to suppose that the reported differences in signal detection properties of the same cell types in areas 17 and 18 for in-phase motion of a bar and superimposed noise reflect the different spatial frequency ranges of the noise processes used in different studies, rather than representing a genuine areal difference. Comparisons of threshold signal-to-noise ratios of the different cell types in each area for a moving bar and a superimposed *stationary* noise field strengthen this conclusion: simple cells in areas 17 and 18 have comparable detection thresholds, which are much higher than those of complex cells (Hoffmann and von Seelen, 1978; Dinse and von Seelen, 1981b). The minority of cells classified as simple by Dinse and von Seelen (1981b) which had intermediate thresholds for the detection of a moving bar embedded in stationary noise may have been B-cells, since cell classification was based on presence or absence of inhibitory sidebands.

Suppression of responses to a moving foreground spot by in-phase motion of background texture has been reported for cells in cat superior colliculus (Mason, 1979; Fromel, 1980a,b) and lateral suprasylvian (LS) cortex (von Grunau and Frost, 1983). The magnitude of in-phase suppression described by the latter authors is comparable to that seen in area 18 cells when bars of suboptimal length are used. However, in both superior colliculus (Fromel, 1980a,b) and the LS area (von Grunau and Frost, 1983), antiphase motion of foreground spot and background texture caused reduced suppression or response facilitation. Hammond

and MacKay (1981b) also reported that the suppressive effects of synchronously moving backgrounds on bar responses of area 17 simple cells were greater for in-phase than for antiphase motion. Further, in the LS area, magnitude of in-phase suppression and antiphase facilitation varies with the direction of background motion (von Grunau and Frost, 1983), while in superior colliculus the magnitude of in-phase and antiphase modulation varies with the relative velocity between spot and background texture (Frome, 1980a,b). Thus, no description of noise-insensitive cells in area 18 will be complete without additional tests in which bar and background are moved at different relative velocities, both in-phase and in antiphase, over a range of directions.

8.4. CONCLUSION

In the present study, the use of both oriented and textured stimuli has revealed striking similarities between area 17 and area 18. Confirming previous work (Tretter et al., 1975; Henry, 1977; Henry et al., 1978b, 1979; Harvey, 1980a,b; Ferster, 1981; Orban and Kennedy, 1981), areas 17 and 18 contained similar cell types, which showed comparable differences in secondary response properties. Thus overall, C-cells more often received strong binocular drive than S-cells, and had lower spontaneous activity than either S- or B-cells. S-cells in each area were predominantly direction-selective. In addition, quantitative comparisons confirmed that in each area, C-cells had comparable directional tuning which was significantly broader than that of B- or S-cells. S-cells had the narrowest directional tuning, though those in area 18 were more broadly tuned than those in area 17. In the present study, the similarity between areas 17 and 18 has been shown to extend to the noise sensitivity of different cell types and the association for cells within a class between noise sensitivity and receptive field properties. S-cells were predominantly noise-insensitive, while C-cells were more sensitive to noise than B-cells, but showed variation in noise sensitivity, which was associated

with other response properties: strongly noise-sensitive C-cells had broader directional tuning and higher spontaneous activity than other C-cells, and were more often strongly binocularly-driven and direction-selective. However in area 18, as in area 17 (Hammond and Smith 1983, 1984), deep-layer C-cells were more noise-sensitive as a group than superficial-layer C-cells, and showed a stronger association between noise sensitivity and response properties. Among B-cells in each area, those sensitive to noise had relatively wide receptive fields and were unique in being spontaneously active.

In both areas 17 and 18, preferred directions for noise and bar motion were dissimilar in all cells. Tuning for noise was labile and varied with velocity, while tuning for bar motion was usually velocity invariant. In each area, a significant proportion of noise-sensitive cells showed variations in tuning for bar motion with velocity, which were associated with the velocity-dependent changes in tuning for noise, though there was some indication that cells with labile bar tuning are more common in area 18 than in area 17. A comparably high proportion of noise-sensitive cells in areas 17 and 18 showed asymmetrical tuning for motion of a long bar, with broader tuning on the flank closest to the preferred direction for noise. In asymmetrically tuned cells from each area in which the appropriate comparisons were made, preferred direction for a spot shifted away from the preferred direction for a bar towards that for noise.

As in area 17 simple cells (Hammond and MacKay 1981b), area 18 cells which were not driven by noise motion alone showed suppression of responses to foreground bars by synchronous motion of background noise. In view of this finding and the comparable sensitivity of C-cells in areas 17 and 18 to noise motion alone, it was argued that the previously reported differences between the same cell types in the two areas in detection thresholds for a bar moving in-phase with a superimposed field of visual noise are attributable to the use of a noise process in area 18 with inappropriate spatial frequency characteristics (Dinse and von Seelen 1981b).

Thus, results from the present study in which both bars and visual noise were

used as stimuli emphasize the overall similarity in neuronal organization of areas 17 and 18 and thus confirm and extend previous work. They are in line with other evidence that the two cortical areas process information in parallel. Thus, the laminar distribution of different cell types is similar in areas 17 and 18, as is the association between cell type and synaptic distance from the thalamus (Singer et al., 1975; Tretter et al., 1975; Henry et al., 1979; Bullier and Henry, 1979a,b,c; Harvey, 1980a,b; Ferster, 1981; Orban and Kennedy, 1981; Martin and Whitteridge, 1984). In area 17 and area 18, cortico-thalamic projections arise from layer VI (Gilbert and Kelly, 1975; Lund et al., 1979; Harvey, 1980b; Tsumoto and Suda, 1980), while layer V is the source of subcortical projections to the superior colliculus, the NOT, the pons and the pulvinar (Hollander, 1974; Palmer and Rosenquist, 1974; Gilbert and Kelly, 1975; Magalhães-Castro et al., 1975; Gibson et al., 1976; Albus and Donate-Oliver, 1977; Kawamura and Chiba, 1979; Lund et al., 1979; Harvey, 1980b; Albus et al., 1981; Schoppmann, 1981). In both areas, B- and C-cells project to the thalamus (Harvey, 1980a; Tsumoto and Suda, 1980), while layer V cells which project to pre-oculomotor structures have properties typical of strongly noise-sensitive, deep-layer C-cells recorded in the present study (Palmer and Rosenquist, 1974; Gibson et al., 1978; Harvey, 1980b; Schoppmann, 1981).

Areas 17 and 18 contain a similar proportion of cells with monosynaptic input from the thalamus (Singer et al., 1977; Tretter et al., 1975), and the properties of area 18 cells do not depend on the functional integrity of area 17 (Dreher and Cotter, 1975; Sherk, 1978c). Indeed there are strong *reciprocal* connections between areas 17 and 18 (Bullier and Kennedy, 1984b; Symonds and Rosenquist, 1984a). From a consideration of visual cortico-cortical connections in the monkey, Orban (1984) has argued that reciprocal connections between two cortical areas which are asymmetrical in their lamination (i.e., in which the input layers are different from the output layers) are vital to the processing of information, whereas more symmetrical connections are not necessary for normal functioning of an area. In this context, there is recent evidence that cortico-cortical projections from areas

17 and 18 arise predominantly from the supragranular layers, while projections towards these areas originate predominantly or exclusively in the infragranular layers (Bullier et al., 1984b; Symonds and Rosenquist, 1984b). On the other hand, connections *between* areas 17 and 18 originate and terminate in most layers, but predominantly in the superficial layers (Bullier et al., 1984b,c; Symonds and Rosenquist, 1984b). In the superficial layers, these connections originate from and terminate in discontinuous patches (Gilbert and Kelly, 1975; Gilbert and Wiesel, 1981b; Bullier et al., 1984b; Symonds and Rosenquist, 1984a) and there is some evidence that a given site in one area receives an input from patches to which it projects (Symonds and Rosenquist, 1984a). Thus, there is now overwhelming evidence that areas 17 and 18 are primary visual areas which process information in parallel (cf. Tretter et al., 1975; Orban, 1977).

The major differences between the two areas are that area 18 cells have larger receptive fields (Hubel and Wiesel, 1965), prefer lower spatial frequencies (Movshon et al., 1978c) and respond to higher stimulus velocities (Orban et al., 1981a). Area 18, subserving central vision, has clear superiority in the coding of spatio-temporal parameters such as velocity and direction of motion (Orban et al., 1981a,b). Since psychophysical studies have demonstrated the importance of low spatial frequencies for basic pattern recognition, area 18 would seem not simply to be involved in movement detection (Movshon et al., 1978c), but in the perception of patterns during movement, and thus would have a complementary function to that of area 17. In this context, Burr et al. (1985) have recently shown that the spatial frequency response functions of neurones in area 18 (but not of those in area 17) shift to lower spatial frequencies as velocity is increased, thus paralleling the increase with velocity in relative and absolute sensitivity to low spatial frequencies observed in human psychophysical studies (Burr and Ross, 1982).

What is the source of the major differences between areas 17 and 18? Differences in spatial frequency selectivity in the two areas presumably reflect substantial convergence in the projection from area 17 to area 18 (Gilbert, 1985); the rel-

atively greater degree of thalamo-cortical convergence in area 18 (Geisert, 1985, cf. Leventhal, 1979) and differences in the functional type of thalamic input to the two areas. Y-cells, which provide the predominant thalamic input to area 18, are much more sensitive to low spatial frequencies than are X-cells (Lehmkuhle et al. 1980, Troy, 1983a) which project almost exclusively to area 17. Area 18 receives a more substantial input than area 17 from the MIN (Hollander and Vanegas, 1977, Geisert, 1980), whose Y-cells have larger receptive fields than those in the laminated dLGN (Kratz et al., 1978b, Dreher and Sefton, 1979). Irrespective of their location in the thalamus, Y-cells have more extensive arborizations in area 18 than in area 17 (Humphrey et al., 1985a,b). The recent evidence of Bunbacher and Albus (1987) suggests that only a small proportion of geniculate cells involved in the projection to areas 17 and 18 have axons which branch to supply both areas. Compared with area 17, area 18 receives a greater proportion of its thalamic input from lamina C of the dLGN (Hollander and Vanegas, 1977) while, in the dorsal layers, the greatest concentration of area 18-projecting cells is found in the ventral part of lamina A1 (Geisert, 1985). Significantly, lamina C Y-cells are more sensitive than other Y-cells in the dLGN, particularly at low spatial frequencies (Frascella and Lehmkuhle, 1984), and Y-cells located ventrally in lamina A1 and in lamina C have relatively low spatial resolution and short-latency retinal input (Movshon, 1981). According to Friedlander et al. (1979, 1981) geniculate Y-cells can have either class 1 or class 2 morphology (Guillery, 1966). Since the axons of geniculate cells have conduction velocities which match those of their afferents (Cleland et al., 1971b, 1976, Hoffmann et al., 1972, Wilson et al., 1976, Dreher and Sefton, 1979), and since class 1 cells have larger-calibre axons than class 2 cells (Ferster and LeVay, 1978), geniculate Y-cells with the lowest spatial resolution may be predominantly class 1 cells, and this morphological type provides the Y input to area 18 (LeVay and Ferster, 1977, Meyer and Albus, 1981b). The relatively large dendritic trees of class 1 Y cells (Friedlander et al., 1979, 1981) are presumably able to support a greater degree of excitatory convergence.

Differences in the functional type of thalamic input to areas 17 and 18 proba-

bly play an insubstantial role in determining the differences in velocity sensitivity of the two areas, since these are much greater than those of X- and Y-cells (Orban et al., 1985). Moreover, while the differences in velocity sensitivity of X- and Y-cells are due almost entirely to spatial factors (Hamasaki and Cohen, 1977; Bullier and Norton, 1979b; Lehmkuhle et al., 1980; Lennie, 1980; Cleland and Harding, 1983; Troy, 1983b; Cleland and Lee, 1985), temporal factors would seem to be more important in determining the differences in velocity sensitivity of areas 17 and 18 (Movshon et al., 1978c; Duysens et al., 1985a,b). In this context, however, it is noteworthy that Y-cells in the laminated dLGN with the lowest spatial resolution and shortest-latency retinal input also have the highest temporal resolution (Movshon, 1981), and it was argued that these cells provide a substantial input to area 18.

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REFERENCES

Ahlsen, G., Lindstrom, S. (1982) Excitation of perigeniculate neurones via axon collaterals of principal cells. *Brain Res.* **236**: 477–481.

Ahlsen, G., Lindstrom, S., Lo, F.-S. (1983) Excitation of perigeniculate neurones from X and Y principal cells in the lateral geniculate nucleus of the cat. *Acta Physiol. Scand.* **118**: 445–448.

Ahlsen, G., Lindstrom, S., Lo, F.-S. (1985) Interaction between inhibitory pathways to principal cells in the lateral geniculate nucleus of the cat. *Exp. Brain Res.* **58**: 134–143.

Ahmed, B., Hammond, P. (1983) Response of cat retinal ganglion cells to motion of visual texture. *Exp. Brain Res.* **53**: 444–450.

Ahmed, B., Hammond, P. (1984) Directional tuning of cat visual cortical cells for oriented foreground stimuli: influence of non-uniform stationary textured backgrounds. *J. Physiol.* **351**: 12P.

Ahmed, B., Hammond, P., Nothdurft, H.-C. (1977) A reappraisal of the feline mesopic range. *J. Physiol.* **266**: 94P.

Albus, K. (1975) Predominance of monocularly driven cells in the projection area of the central visual field in cat's striate cortex. *Brain Res.* **89**: 341–347.

Albus, K., Donate-Oliver, F. (1977) Cells of origin of the occipito-pontine projection in the cat: functional properties and intracortical location. *Exp. Brain Res.* **28**: 167–174.

Albus, K., Donate-Oliver, F., Sanides, D., Fries, W. (1981) The distribution of pontine projection cells in visual and association cortex of the cat: an experimental study with horseradish peroxidase. *J. Comp. Neurol.* **201**: 175–189.

Albus, K., Fries, W. (1980) Inhibitory sidebands of complex receptive fields in the cat's striate cortex. *Vis. Res.* **20**, 369–372.

Anderson, J., Gabbott, P., Martin, K. A. C., Whitteridge, D. (1986) The function and intracortical connectivity of a Meynert cell in area 17 of the cat visual cortex. *J. Physiol.* **371**, 41P.

Andrews, B. W., Pollen, D. A. (1979) Relationship between spatial frequency selectivity and receptive field profile of simple cells. *J. Physiol.* **287**, 163–176.

Andrews, D. P., Hammond, P. (1970) Mesopic increment threshold spectral sensitivity of single optic tract fibres in cat, under mesopic adaptation: cone-rod interaction. *J. Physiol.* **209**, 65–81.

Baker, J., Gibson, A., Mower, G., Robinson, F., Glickstein, M. (1983) Cat visual cortico-pontine cells project to the superior colliculus. *Brain Res.* **265**, 227–232.

Barlow, H. B., Blakemore, C., Pettigrew, J. D. (1967) The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

Barlow, H. B., Derrington, A. M., Harris, L. R., Lennie, P. (1977) The effects of remote retinal stimulation on the responses of cat retinal ganglion cells. *J. Physiol.* **269**, 177–194.

Bellhorn, R. W., Aquirre, G. D., Bellhorn, M. B. (1974) Feline central retinal degeneration. *Invest. Opthalmol.* **13**, 608–616.

Berman, N., Jones, E. G. (1977) A retino-pulvinar projection in the cat. *Brain Res.* **134**, 237–248.

Berman, N., Payne, B. R., Labar, D. R., Murphy, E. H. (1982) Functional organization of neurons in cat striate cortex: variations in ocular dominance and receptive-field type with cortical lamminae and location in the visual field. *J. Neurophysiol.* **48**, 1362–1377.

Berson, D M., Graybiel, A M. (1978). Parallel thalamic zones in the LP-pulvinar complex of the cat identified by their afferent and efferent connections. *Brain Res.* **147**, 139–148.

Birnbacher, D., Albus, K. (1987). Divergence of single axons in afferent projections to the cat's visual cortical areas 17, 18, and 19: A parametric study. *J. Comp. Neurol.* **261**, 543–561.

Bishop, P O., Coombs, J., Henry, G H. (1973). Receptive fields of simple cells in the cat striate cortex. *J. Physiol.* **231**, 31–60.

Bishop, P O., Kato, H., Orban, G A. (1980). Direction-selective cells in complex family in cat striate cortex. *J. Neurophysiol.* **43**, 1266–1283.

Bisti, S., Carmignoto, G., Galli, L., Maffei, L. (1985). Spatial-frequency characteristics of neurones of area 18 in the cat: dependence on the velocity of the visual stimulus. *J. Physiol.* **359**, 279–298.

Blomfield, S. (1974). Arithmetical operations performed by nerve cells. *Brain Res.* **69**, 115–124.

Bodnis-Wollner, I G., Pollen, D A., Ronner, S F. (1976). Responses of complex cells in the visual cortex of the cat as a function of the length of moving slits. *Brain Res.* **116**, 205–216.

Bolz, J., Rosner, G., Wassle, H. (1982). Response latency of brisk-sustained (X) and brisk-transient (Y) cells in the cat retina. *J. Physiol.* **328**, 171–190.

Bowling, D B., Michael, C R. (1980). Projection patterns of single physiologically characterized optic tract fibres in cat. *Nature* **286**, 899–902.

Bowling, D B., Michael, C R. (1984). Terminal patterns of single physiologically characterized optic tract fibers in the cat's lateral geniculate nucleus. *J. Neurosci.* **4**, 198–216.

Boyapati, J., Henry, G.H. (1987) The duplex character of the corticofugal pathway from the striate cortex to the lateral geniculate complex of the cat. *Vis. Res.* **27**, 5, 723–726.

Boycott, B.B., Wassle, H. (1974) The morphological types of ganglion cells of the domestic cat's retina. *J. Physiol.* **240**, 397–419.

Bullier, J., Henry, G.H. (1979a) Ordinal position of neurons in cat striate cortex. *J. Neurophysiol.* **42**, 1251–1263.

Bullier, J., Henry, G.H. (1979b) Neural path taken by afferent streams in striate cortex of the cat. *J. Neurophysiol.* **42**, 1264–1270.

Bullier, J., Henry, G.H. (1979c) Laminar distribution of first-order neurons and afferent terminals in cat striate cortex. *J. Neurophysiol.* **42**, 1271–1281.

Bullier, J., Kennedy, H., Salinger, W. (1984a) Bifurcation of subcortical afferents to visual areas 17, 18, and 19 in the cat cortex. *J. Comp. Neurol.* **228**, 309–328.

Bullier, J., Kennedy, H., Salinger, W. (1984b) Branching and laminar origin of projections between visual cortical areas in the cat. *J. Comp. Neurol.* **228**, 329–341.

Bullier, J., McCourt, M., Henry, G.H. (1984c) Cortico-cortical connections between area 17 and areas 18 and 19 in the cat cortex. Anatomy and physiology. *Neurosci. Lett. Suppl.* **18**, S69.

Bullier, J., Norton, T.T. (1979a) X and Y relay cells in cat lateral geniculate nucleus. Quantitative analysis of receptive-field properties and classification. *J. Neurophysiol.* **42**, 244–273.

Bullier, J., Norton, T.T. (1979b) Comparison of receptive-field properties of X and Y ganglion cells with X and Y lateral geniculate cells in the cat. *J. Neurophysiol.* **42**, 274–291.

Burr, D.C., Morrone, C., Maffei, L. (1981) Intra-cortical inhibition prevents sim-

ple cells from responding to textured visual patterns. *Exp. Brain Res.* **43** 455–458.

Burr, D.C., Ross, J. (1982). Contrast sensitivity at high velocities. *Vis. Res.* **22** 479–484.

Burrows, G. R., Hayhow, W.R. (1971). The organization of the thalamo-cortical visual pathways in the cat. *Brain Behav. Evol.* **4** 220–272.

Cleland, B.G. (1983). Sensitivity to stationary flashing spots of the brisk classes of ganglion cells in the cat retina. *J. Physiol.* **345** 15–26.

Cleland, B.G., Dubin, M.W., Levick, W.R. (1971a). Simultaneous recording of input and output of lateral geniculate neurones. *Nature* **231** 191–192.

Cleland, B.G., Dubin, M.W., Levick, W.R. (1971b). Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *J. Physiol.* **217** 473–496.

Cleland, B.G., Harding, T.H. (1983). Response to the velocity of moving visual stimuli of the brisk classes of ganglion cells in the cat's retina. *J. Physiol.* **345** 47–64.

Cleland, B.G., Harding, T.H., Tulunay-Keesey, U. (1979). Visual resolution and receptive field size: examination of two kinds of cat retinal ganglion cell. *Science* **205** 1015–1017.

Cleland, B.G., Lee, B.B. (1985). A comparison of visual responses of cat lateral geniculate nucleus neurones with those of ganglion cells afferent to them. *J. Physiol.* **369** 249–268.

Cleland, B.G., Lee, B.B., Vidyasagar, T.R. (1983). Responses of neurons in the cat's lateral geniculate nucleus to moving bars of different length. *J. Neurosci.* **3** 108–116.

Cleland, B.G., Levick, W.R. (1974a). Brisk and sluggish concentrically organized ganglion cells in the cat's retina. *J. Physiol.* **240** 421–456.

Cleland, B G., Levick, W R (1974b) Properties of rarely encountered types of ganglion cells in the cat's retina and an overall classification *J Physiol* **240** 457–492

Cleland, B G , Levick, W R , Morstyn, R Wagner, H G (1976) Lateral geniculate relay of slowly conducting retinal afferents to cat visual cortex *J Physiol* **255** 299–320

Cleland, B G , Levick, W R , Sanderson, K J (1973) Properties of sustained and transient ganglion cells in the cat's retina *J Physiol* **228** 649–680

Cleland, B G , Levick, W R , Wassle, H (1975a) Physiological identification of a morphological class of ganglion cell *J Physiol* **248** 151–171

Cleland, B G., Morstyn, R Wagner, H G , Levick, W R (1975b) Long latency input to lateral geniculate neurones of the cat *Brain Res* **91** 309–310

Cohen, H I , Winters, R W Hamasaki, D I (1980) Response of X and Y cat retinal ganglion cells to moving stimuli *Exp Brain Res* **38** 299–303

Colonnier, M (1968) Synaptic patterns on different cell types in the different laminae of the cat visual cortex An electron microscopic study *Brain Res* **9** 268–287

Creutzfeldt, O D , Garey, L J , Kuroda, R , Wolff, J -R (1977) The distribution of degenerating axons after small lesions in the intact and isolated visual cortex of the cat *Exp Brain Res* **27** 419–440

Creutzfeldt, O D , Ito, M (1968) Functional synaptic organization of primary visual cortex neurones in the cat *Exp Brain Res* **6** 324–352

Creutzfeldt, O D , Kuhnt, U , Benevento, L A (1974) An intracellular analysis of visual cortical neurones to moving stimuli responses in a co-operative neuronal network *Exp Brain Res* **21** 251–274

Curtis, D.R., Tebecis, A.K. (1972): Bicuculline and thalamic inhibition. *Exp. Brain Res.* **16** 210–218.

Davis, T.L., Sterling, P. (1979): Microcircuitry of the cat visual cortex: Classification of neurones in layer IV of area 17, and identification of the patterns of lateral geniculate input. *J. Comp. Neurol.* **188** 599–628.

Dean, A.F., Hess, R.F., Tolhurst, D.J. (1980): Divisive inhibition involved in direction selectivity. *J. Physiol.* **308** 84–85P.

Dean, A.F., Tolhurst, D.J. (1983): On the distinctiveness of simple and complex cells in the visual cortex of the cat. *J. Physiol.* **344** 305–325.

DeFelipe, J., Fairén, A. (1982): A type of basket cell in superficial layers of the cat visual cortex. A Golgi-Electron microscope study. *Brain Res.* **244** 9–16.

Derrington, A.M., Fuchs, A.F. (1979): Spatial and temporal properties of X and Y cells in the cat lateral geniculate nucleus. *J. Physiol.* **293** 347–364.

Derrington, A.M., Lennie, P. (1982): The influence of temporal frequency and adaptation level on receptive field organization of retinal ganglion cells in cat. *J. Physiol.* **333** 343–366.

Derrington, A.M., Lennie, P., Wright, M.J. (1979): The mechanism of peripherally evoked response in retinal ganglion cells. *J. Physiol.* **289** 299–310.

DeValois, R.L., Yund, E.W., Hepler, N. (1982): The orientation and direction selectivity of cells in macaque visual cortex. *Vis. Res.* **22** 531–544.

Dinse, H.R.O., von Seelen, W. (1981a): On the function of cell systems in area 18. Part I. *Biol. Cybern.* **41** 47–57.

Dinse, H.R.O., von Seelen, W. (1981b): On the function of cell systems in area 18. Part II. *Biol. Cybern.* **41** 59–69.

Donaldson, I. L. M., Nash, J. R. G. (1975a) Variability of the relative preference for stimulus orientation and direction of movement in some units of the cat visual cortex (areas 17 and 18). *J. Physiol.* **245**: 305–324.

Donaldson, I. L. M., Nash, J. R. G. (1975b) The effect of a chronic lesion in cortical area 17 on the visual responses of units in area 18 of the cat. *J. Physiol.* **245**: 325–332.

Dreher, B. (1972) Hypercomplex cells in the cat's striate cortex. *Invest. Opthalmol.* **11**: 355–356.

Dreher, B., Cotter, L. J. (1975) Visual receptive-field properties of cells in area 18 of cat's cerebral cortex before and after acute lesions in area 17. *J. Neurophysiol.* **38**: 735–750.

Dreher, B., Leventhal, A. G., Hale, P. T. (1980) Geniculate input to cat visual cortex: A comparison of area 19 with areas 17 and 18. *J. Neurophysiol.* **44**: 804–826.

Dreher, B., Sefton, A. J. (1975) Receptive field properties of cells in the cat's medial interlaminar nucleus (MIN). *Proc. Aust. Physiol. Pharmacol. Soc.* **6**: 209.

Dreher, B., Sefton, A. J. (1979) Properties of neurons in cat's dorsal lateral geniculate nucleus: a comparison between medial interlaminar and laminated parts of the nucleus. *J. Comp. Neurol.* **183**: 47–64.

Dubin, M. W., Cleland, B. G. (1977) Organization of visual inputs to interneurons of lateral geniculate nucleus of the cat. *J. Neurophysiol.* **40**: 410–427.

Duysens, J., Orban, G. A., Cremieux, J. (1984) Functional basis for the preference for slow movement in area 17 of the cat. *Vis. Res.* **24**: 17–24.

Duysens, J., Orban, G. A., Cremieux, J. (1985a) Velocity selectivity in the cat visual system. II. Independence from interactions between different loci. *J. Neurophysiol.* **54**: 1050–1067.

Duysens, J., Orban, G. A., Cremieux, J., Maes, H. (1985b). Velocity selectivity in the cat visual system. III. Contribution of temporal factors. *J. Neurophysiol.* **54**: 1068–1083.

Duysens, J., Orban, G. A., Verbeke, O. (1982). Velocity sensitivity mechanisms in cat visual cortex. *Exp. Brain Res.* **45**: 287–294.

Eccles, J. C. (1964). *The physiology of synapses*. Springer-Verlag, Berlin.

Einstein, G., Davis, T. L., Sterling, P. (1987). Ultrastructure of synapses from the A-lamina of the lateral geniculate nucleus in layer IV of the cat striate cortex. *J. Comp. Neurol.* **260**: 63–75.

Enroth-Cugell, C., Robson, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**: 517–552.

Enroth-Cugell, C., Robson, J. G., Schweitzer-Tong, D. E., Watson, A. B. (1983). Spatio-temporal interactions in cat retinal ganglion cells showing linear spatial summation. *J. Physiol.* **341**: 279–307.

Enroth-Cugell, C., Shapley, R. M. (1975a). Adaptation and dynamics of cat retinal ganglion cells. *J. Physiol.* **233**: 271–309.

Enroth-Cugell, C., Shapley, R. M. (1973b). Flux, not retinal illumination, is what retinal ganglion cells really care about. *J. Physiol.* **233**: 311–326.

Famiglietti, E. V. (1970). Dendro-dendritic synapses in the lateral geniculate nucleus of the cat. *Brain Res.* **20**: 181–191.

Famiglietti, E. V., Peters, A. (1972). The synaptic glomerulus and the intrinsic neuron in the dorsal lateral geniculate nucleus of the cat. *J. Comp. Neurol.* **144**: 285–334.

Fernald, R., Chase, R. (1971). An improved method for plotting retinal landmarks and focusing the eyes. *Vis. Res.* **11**: 95–96.

Ferster, D. (1981). A comparison of binocular depth mechanisms in areas 17 and 18 of the cat visual cortex. *J. Physiol.* **311**, 623–655.

Ferster, D., LeVay, S. (1978). The axonal arborizations of lateral geniculate neurons in the striate cortex of the cat. *J. Comp. Neurol.* **182**, 923–944.

Ferster, D., Lindstrom, S. (1983). An intracellular analysis of geniculo-cortical connectivity in area 17 of the cat. *J. Physiol.* **342**, 181–215.

Ferster, D., Lindstrom, S. (1985). Synaptic excitation of neurones in area 17 of the cat by intracortical axon collaterals of cortico-geniculate cells. *J. Physiol.* **367**, 233–252.

Fischer, B., Kruger, J. (1974). The shift-effect in the cat's lateral geniculate nucleus. *Exp. Brain Res.* **21**, 225–227.

Fischer, B., Kruger, J., Droll, W. (1975). Quantitative aspects of the shift-effect in cat retinal ganglion cells. *Brain Res.* **83**, 391–403.

Fitzpatrick, D., Penny, G. R., Schmechel, D. E. (1984). Glutamic acid decarboxylase-immunoreactive neurons and terminals in the lateral geniculate nucleus of the cat. *J. Neurosci.* **4**, 1809–1829.

Frascella, J., Lehmkuhle, S. (1984). A comparison between Y cells in A laminae and lamina C of cat dorsal lateral geniculate nucleus. *J. Neurophysiol.* **52**, 911–920.

Freund, T. F., Martin, K. A. C., Somogyi, P., Whitteridge, D. (1985b). Innervation of cat visual areas 17 and 18 by physiologically identified X- and Y-type thalamic afferents. II. Identification of postsynaptic targets by GABA immunocytochemistry and Golgi impregnation. *J. Comp. Neurol.* **242**, 275–291.

Freund, T. F., Martin, K. A. C., Whitteridge, D. (1985a). Innervation of cat visual areas 17 and 18 by physiologically identified X- and Y-type thalamic afferents. I. Arborization patterns and quantitative distribution of postsynaptic elements.

J Comp Neurol **242** 263-274

Friedlander, M J., Lin, C.-S., Sherman, S M. (1979) Structure of physiologically identified X and Y cells in the cat s lateral geniculate nucleus. *Science* **204** 1114-1117

Friedlander, M J., Lin, C., Stanford, L R., Sherman, S M. (1981) Morphology of functionally identified neurons in lateral geniculate nucleus of the cat. *J Neurophysiol* **46** 80-129

Frishman, L J., Schweitzer-Tong, D E., Goldstein, E B. (1983) Velocity tuning of cells in dorsal lateral geniculate nucleus and retina of the cat. *J Neurophysiol* **50** 1393-1414

Fromel, G. (1980a) Extraction of objects from structured backgrounds in the cat superior colliculus. Part I. *Biol Cybern* **38** 63-73

Fromel, G. (1980b) Extraction of objects from structured backgrounds in the cat superior colliculus. Part II. *Biol Cybern* **38** 75-83

Fukuda, Y., Stone, J. (1974) Retinal distribution and central projections of Y-, X-, and W-cells of the cat s retina. *J Neurophysiol* **37** 749-772

Fukuda, Y., Stone, J. (1976) Evidence of differential inhibitory influences on X- and Y-type relay cells in the cat's lateral geniculate nucleus. *Brain Res* **113** 188-196

Gabbott, P L A., Martin, K A C., Whitteridge, D. (1987) Connections between pyramidal neurons in layer 5 of cat visual cortex (area 17). *J Comp Neurol* **259** 304-315

Garey, L J. (1971) A light and electron microscopic study of the visual cortex of the cat and monkey. *Proc R Soc Lond* **B179** 21-40

Garey, L J., Powell, T P. (1967) The projection of the lateral geniculate nucleus

upon the cortex in the cat. *Proc. R. Soc. Lond.* **B169** 107–126.

Garey, L.J., Powell, T.P. (1971): An experimental study of the termination of the lateral geniculo-cortical pathway in the cat and monkey. *Proc. R. Soc.* **B179** 41–63.

Geisert, E.E. (1980): Cortical projections of the lateral geniculate nucleus in the cat. *J. Comp. Neurol.* **190** 793–812.

Geisert, E.E. (1985): The projection of the lateral geniculate nucleus to area 18. *J. Comp. Neurol.* **238** 101–106.

Gibson, A., Baker, J., Mower, G., Glickstein, M. (1978): Corticopontine cells in area 18 of the cat. *J. Neurophysiol.* **41** 484–495.

Gibson, A., Mower, G., Baker, J., Glickstein, M. (1976): Corticopontine visual cells in the cat. *Soc. Neurosci. Abstr.* **2** 1112.

Gibson, J.J. (1950): *The perception of the visual world.* Boston, Mass.: Houghton Mifflin.

Gibson, J.J. (1966): *The senses considered as perceptual systems.* Boston, Mass.: Houghton Mifflin.

Gilbert, C.D. (1977): Laminar differences in receptive field properties of cells in cat primary visual cortex. *J. Physiol.* **268** 391–421.

Gilbert, C.D. (1985): Horizontal integration in the neocortex. *Trends Neurosci.* **8** 160–165.

Gilbert, C.D., Kelly, J.P. (1975): The projections of cells in different layers of the cat's visual cortex. *J. Comp. Neurol.* **163** 81–106.

Gilbert, C.D., Wiesel, T.N. (1979): Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. *Nature* **280** 120–125.

Gilbert, C D , Wiesel, T N. (1981a). Laminar specialization and intracortical connections in cat primary visual cortex. In Schmitt, F O , Worden, F G , Adelman, G , Dennis, S G (eds). *The organisation of the cerebral cortex*. MIT Press, Cambridge, Mass , pp163–191

Gilbert, C D , Wiesel, T N (1981b). Projection bands in visual cortex. *Soc Neurosci Abstr* **7** 359

Gilbert, C D , Wiesel, T N (1983). Clustered intrinsic connections in cat visual cortex. *J Neurosci* **3** 1116–1133

Glezer, V D , Tscherbach, T A , Gauselman, V E , Bondarko, V M (1980). Linear and non-linear properties of simple and complex receptive fields in area 17 of the cat visual cortex. *Biol Cybern* **37** 195–208

Goodwin, A W , Henry, G H (1978). The influence of stimulus velocity on the responses of single neurones in the striate cortex. *J Physiol* **277** 467–482

Gray, E G (1959). Axo-somatic and axo-dendritic synapses of the cerebral cortex: an electron microscope study. *J Anat* **93** 420–433

Graybiel, A M , Berson, D M (1980). Autoradiographic evidence for a projection from the pretectal nucleus of the optic tract to the dorsal lateral geniculate nucleus complex in the cat. *Brain Res* **195** 1–12

Guillery, R W (1966). A study of Golgi preparations from the dorsal lateral geniculate nucleus of the adult cat. *J Comp Neurol* **128** 21–50

Guillery, R W (1970). The laminar distribution of retinal fibers in the dorsal lateral geniculate nucleus of the cat: a new interpretation. *J Comp Neurol* **138** 339–368

Guillery, R W , Geisert, E E , Polley, E H , Mason, C A (1980). An analysis of the retinal afferents to the cat's medial interlaminar nucleus and to its rostral

thalamic extension the geniculate wing. *J. Comp. Neurol.* **194**: 117–142.

Gulyás, B., Orban, G.A., Duysens, J., Maes, H. (1987). The suppressive influence of moving textured backgrounds on responses of cat striate neurons to moving bars. *J. Neurophysiol.* **57**: 1767–1791.

Hamasaki, D.I., Cohen, H.I. (1977). Differential response of X and Y retinal ganglion cells to moving stimuli: results from a difference in the surround mechanism. *Brain Res.* **122**: 157–161.

Hammond, P. (1973). Contrasts in spatial organization of receptive fields at geniculate and retinal levels: Centre, surround and outer surround. *J. Physiol.* **228**: 115–137.

Hammond, P. (1974). Cat retinal ganglion cells: size and shape of receptive field centres. *J. Physiol.* **242**: 99–118.

Hammond, P. (1977). Receptive field mechanisms of sustained and transient retinal ganglion cells in the cat. *J. Physiol.* **23**: 113–128.

Hammond, P. (1978a). On the use of nitrous oxide/oxygen mixtures for anaesthesia in cats. *J. Physiol.* **275**: 64P.

Hammond, P. (1978b). Inadequacy of nitrous oxide/oxygen mixtures for maintaining anaesthesia in cats: satisfactory alternatives. *Pain* **5**: 143–151.

Hammond, P. (1978c). Directional tuning of complex cells in area 17 of the feline visual cortex. *J. Physiol.* **285**: 479–491.

Hammond, P. (1980). A semi-chronic preparation for cortical recording. *J. Physiol.* **298**: 3–4P.

Hammond, P. (1981a). Simultaneous determination of directional tuning of complex cells in cat striate cortex for bar and for texture motion. *Exp. Brain Res.* **41**: 364–369.

Hammond, P. (1981b): Non-stationarity of ocular dominance in cat striate cortex. *Exp. Brain Res.* **42** 189–195.

Hammond, P., Ahmed, B. (1985): Length summation of complex cells in cat striate cortex: a reappraisal of the "special/standard" classification. *Neurosci.* **15** 639–649.

Hammond, P., Ahmed, B., Smith, A.T. (1986): Relative motion sensitivity in cat striate cortex as a function of stimulus direction. *Brain Res.* **386** 93–104.

Hammond, P., Andrews, D.P. (1978): Orientation tuning of cells in areas 17 and 18 of the cat's visual cortex. *Exp. Brain Res.* **31** 341–351.

Hammond, P., Andrews, D.P., James, C.R. (1975): Invariance of orientational and directional tuning in visual cortical cells of the adult cat. *Brain Res.* **96** 56–59.

Hammond, P., MacKay, D.M. (1975): Differential responses of cat visual cortical cells to textured stimuli. *Exp. Brain Res.* **22** 427–430.

Hammond, P., MacKay, D.M. (1977): Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Exp. Brain Res.* **30** 275–296.

Hammond, P., MacKay, D.M. (1981a): Suppressive effects of luminance gradient reversal on simple cells in cat striate cortex. *J. Physiol.* **315** 30P.

Hammond, P., MacKay, D.M. (1981b): Modulatory influences of moving textured backgrounds on responsiveness of simple cells in feline striate cortex. *J. Physiol.* **319** 431–442.

Hammond, P., MacKay, D.M. (1983a): Effects of luminance gradient reversal on complex cells in cat striate cortex. *Exp. Brain Res.* **49** 453–456.

Hammond, P., MacKay, D.M. (1983b): Influence of luminance gradient reversal on simple cells in feline striate cortex. *J. Physiol.* **337** 69–87.

Hammond, P., MacKay, D.M. (1985): Influence of luminance gradient reversal on complex cells in feline striate cortex. *J. Physiol.* **359** 315–329.

Hammond, P., Mouat, G. V. (1986): Influence of stimulus length on directional bias of complex cells in cat striate cortex. *Neurosci.* **18** 25–30.

Hammond, P., Reck, J. (1980a): A method for the simultaneous determination of directional tuning of visual cortical cells for two dissimilar stimuli. *J. Physiol.* **298** 4–5P.

Hammond, P., Reck, J. (1980b): Influence of velocity on directional tuning of complex cells in cat striate cortex for texture motion. *Neurosci. Lett.* **19** 309–314.

Hammond, P., Shorrocks, I.M.E. (1987): Stimulus-dependent characteristics of complex cells in cat striate cortex. *J. Physiol.* **382** 174P.

Hammond, P., Smith, A.T. (1982): On the sensitivity of complex cells in feline striate cortex to relative motion. *Exp. Brain Res.* **47** 457–460.

Hammond, P., Smith, A.T. (1983): Directional tuning interactions between moving oriented and textured stimuli in complex cells of feline striate cortex. *J. Physiol.* **342** 35–49.

Hammond, P., Smith, A.T. (1984): Sensitivity of complex cells in cat striate cortex to relative motion. *Brain Res.* **301** 287–298.

Hanker, J., Yates, P.E., Meltz, C.B., Rustioni, A. (1977): A new specific, sensitive and non-carcinogenic reagent for the demonstration of horseradish peroxidase. *J. Histochem.* **9** 789–792.

Harvey, A.R. (1980a): The afferent connections and laminar distribution of cells in area 18 of the cat. *J. Physiol.* **302** 483–505.

Harvey, A.R. (1980b): A physiological analysis of subcortical and commissural projections of areas 17 and 18 of the cat. *J. Physiol.* **302** 507–534.

Heggelund, P., Albus, K. (1978). Response variability and orientation discrimination of single cells in striate cortex of the cat. *Exp. Brain Res.* **32** 197–211.

Heggelund, P., Moors, J. (1983). Orientation selectivity and the spatial distribution of enhancement and suppression in receptive fields of cat striate cortex cells. *Exp. Brain Res.* **52** 235–247.

Henry, G.H. (1977). Receptive field classes of cells in the striate cortex of the cat. *Brain Res.* **133** 1–28.

Henry, G.H., Bishop, P.O., Dreher, B. (1974a). Orientation, axis and direction as stimulus parameters for striate cells. *Vis. Res.* **14** 767–777.

Henry, G.H., Bishop, P.O., Tupper, R.M., Dreher, B. (1973). Orientation specificity and response variability of cells in the striate cortex. *Vis. Res.* **13** 1771–1779.

Henry, G.H., Dreher, B., Bishop, P.O. (1974b). Orientation specificity of cells in cat striate cortex. *J. Neurophysiol.* **37** 1394–1409.

Henry, G.H., Goodwin, A.W., Bishop, P.O. (1978a). Spatial summation of responses in receptive fields of single cells in cat striate cortex. *Exp. Brain Res.* **32** 245–266.

Henry, G.H., Harvey, A.R., Lund, J. (1979). The afferent connections and laminar distribution of cells in the cat striate cortex. *J. Comp. Neurol.* **187** 725–744.

Henry, G.H., Lund, J., Harvey, A.R. (1978b). Cells of the striate cortex projecting to the Clare-Bishop area of the cat. *Brain Res.* **151** 154–158.

Henry, G.H., Mustari, M.J., Bullier, J. (1983). Different geniculate inputs to B and C cells of cat striate cortex. *Exp. Brain Res.* **52** 179–189.

Hess, R., Negishi, K., Creutzfeldt, O.D. (1975). The horizontal spread of intracortical inhibition in the visual cortex. *Exp. Brain Res.* **22** 415–419.

Hickey, T. L., Guillery, R. W. (1974). An autoradiographic study of retinogeniculate pathways in the cat and the fox. *J. Comp. Neurol.* **156**, 239–254.

Hochstein, S., Shapley, R. M. (1976a). Quantitative analysis of retinal ganglion cell classifications. *J. Physiol.* **262**, 237–264.

Hochstein, S., Shapley, R. M. (1976b). Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. *J. Physiol.* **262**, 265–284.

Hoffmann, K.-P. (1982). Cortical versus subcortical contributions to the optokinetic reflex in the cat. In: Lennerstrand, G., Zee, D., Keller, E. L. (eds.) *Functional basis of ocular motility disorders*, pp. 303–310. Pergamon Press, Oxford.

Hoffmann, K.-P., Bauer, R., Huber, H. P., Mayr, M. (1984). Single cell activity in area 18 of the cat's visual cortex during optokinetic nystagmus. *Exp. Brain Res.* **57**, 118–127.

Hoffmann, K.-P., Morrone, C. M., Reuter, J. H. (1980). A comparison of the responses of single cells in the LGN and visual cortex to bar and noise stimuli in the cat. *Vis. Res.* **20**, 771–777.

Hoffmann, K.-P., Stone, J. (1971). Conduction velocity of afferents to cat visual cortex. A correlation with cortical receptive field properties. *Brain Res.* **32**, 460–466.

Hoffmann, K.-P., Stone, J. (1985). Retinal input to the nucleus of the optic tract of the cat assessed by antidromic activation of ganglion cells. *Exp. Brain Res.* **59**, 395–403.

Hoffmann, K.-P., Stone, J., Sherman, S. M. (1972). Relay of receptive-field properties in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* **35**, 518–531.

Hoffmann, K.-P., von Seelen, W. (1978). Analysis of neuronal networks in the visual system of the cat using statistical signals — simple and complex cells. Part

II *Biol Cybern* **31** 175–185.

Hollander, H. (1974). On the origin of the corticotectal projections in the cat. *Exp Brain Res* **21** 433–439.

Hollander, H., Vanegas, H. (1977). The projection from the lateral geniculate nucleus onto the visual cortex in the cat. A quantitative study with horseradish-peroxidase. *J Comp Neurol* **173** 519–536.

Horn, G., Hill, R.M. (1969). Modification of receptive fields of cells in the visual cortex occurring spontaneously and associated with bodily tilt. *Nature* **221** 186–188.

Hornung, J.P., Garey, L.J. (1981). The thalamic projection to cat visual cortex: Ultrastructure of neurons identified by Golgi impregnation or retrograde horseradish peroxidase transport. *Neurosci* **6** 1053–1068.

Hubel, D.H., Wiesel, T.N. (1961). Integrative action in the cat's lateral geniculate body. *J Physiol* **155** 385–398.

Hubel, D.H., Wiesel, T.N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J Physiol* **160** 106–154.

Hubel, D.H., Wiesel, T.N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. *J Neurophysiol* **28** 229–289.

Hughes, H.C. (1980). Efferent organization of the cat pulvinar complex, with a note on bilateral claustrocortical and reticulocortical connections. *J Comp Neurol* **193** 937–963.

Humphrey, A.L., Sur, M., Uhlrich, D.J., Sherman, S.M. (1985a). Projection patterns of individual X- and Y-cell axons from the lateral geniculate nucleus to cortical area 17 in the cat. *J Comp Neurol* **233** 159–189.

Humphrey, A.L., Sur, M., Uhlrich, D.J., Sherman, S.M. (1985b). Termination

patterns of X- and Y-cell axons in the visual cortex of the cat: projections to area 18, to the 17/18 border region, and to both areas 17 and 18. *J. Comp. Neurol.* **233**: 190–212.

Humphrey, A. L., Weller, R. E. (1985). Functional subgroups among X-cells in the lateral geniculate nucleus of the cat. *Soc. Neurosci. Abstr.* **11**: 318.

Ikeda, H., Wright, M. J. (1972a). Functional organization of the periphery effect in retinal ganglion cells. *Vis. Res.* **12**: 1857–1879.

Ikeda, H., Wright, M. J. (1972b). Receptive field organization of 'sustained' and 'transient' retinal ganglion cells which subserve different functional roles. *J. Physiol.* **227**: 769–800.

Ikeda, H., Wright, M. (1974). Sensitivity of neurones in visual cortex (area 17) under different levels of anaesthesia. *Exp. Brain Res.* **20**: 471–484.

Ikeda, H., Wright, M. (1975). Spatial and temporal properties of 'sustained' and 'transient' neurones in area 17 of the cat's visual cortex. *Exp. Brain Res.* **22**: 363–383.

Illing, R.-B., Wassle, H. (1981). The retinal projection to the thalamus in the cat: a quantitative investigation and a comparison with the retinotectal pathway. *J. Comp. Neurol.* **202**: 265–285.

Itoh, K., Mizuno, N., Sugimoto, T., Nomura, S., Nakamura, Y., Konishi, A. (1979). A cerebello-pulvino-cortical and a retino-pulvino-cortical pathway in the cat as revealed by the use of the anterograde and retrograde transport of horseradish peroxidase. *J. Comp. Neurol.* **187**: 349–378.

Jakiela, H. G., Enroth-Cugell, C., Shapley, R. M. (1976). Adaptation and dynamics in X-cells and Y-cells of the cat retina. *Exp. Brain Res.* **24**: 335–342.

Kaplan, E., Shapley, R. (1982). What controls information processing in the LGN?

Soc. Neurosci. Abstr. **8**:405.

Kaplan, E., Shapley, R. (1984). The origin of the S (Slow) potential in the mammalian lateral geniculate nucleus. *Exp. Brain Res.* **55**: 111–116.

Kato, H., Bishop, P.O., Orban, G.A. (1978). Hypercomplex and the simple/complex cell classifications in cat striate cortex. *J. Neurophysiol.* **41**: 1071–1095.

Kawamura, S., Chiba, M. (1979). Cortical neurons projecting to the pontine nuclei in the cat: An experimental study with the horseradish peroxidase technique. *Exp. Brain Res.* **35**: 269–285.

Kawamura, S., Fukushima, N., Hattori, S. (1979). Topographical origin and ganglion cell type of the retino-pulvinar projection in the cat. *Brain Res.* **173**: 419–429.

Kawamura, S., Sprague, J.M., Niimi, K. (1974). Corticofugal projections from the visual cortices to the thalamus, pretectum and superior colliculus in the cat. *J. Comp. Neurol.* **158**: 339–362.

Kelly, J.P., Gilbert, C.D. (1975). The projections of different morphological types of ganglion cells in the cat's retina. *J. Comp. Neurol.* **163**: 65–80.

Kelly, J.P., van Essen, D.C. (1974). Cell structure and function in the visual cortex of the cat. *J. Physiol.* **238**: 515–547.

Kennedy, H., Baleydier, C. (1977). Direct projections from thalamic intralaminar nuclei to extra-striate visual cortex in the cat traced with horseradish peroxidase. *Exp. Brain Res.* **28**: 133–139.

Kirk, D.L., Cleland, B.G., Wassle, H., Levick, W.R. (1975). Axonal conduction latencies of cat retinal ganglion cells in central and peripheral retina. *Exp. Brain Res.* **23**: 85–90.

Kisvárday, Z.F., Martin, K.A.C., Freund, T.F., Magloczky, Z., Whitteridge, D., Somogyi, P. (1986). Synaptic targets of HRP-filled layer III pyramidal cells in the

cat striate cortex *Exp Brain Res* **64** 541–552

Kisvárday, Z.F., Martin, K.A.C., Friedlander, M.J., Somogyi, P. (1987) Evidence for interlaminar inhibitory circuits in the striate cortex of the cat *J Comp Neurol* **260** 1–19

Kisvárday, Z.F., Martin, K.A.C., Whitteridge, D., Somogyi, P. (1985) Synaptic connections of intracellularly filled clutch cells: a type of small basket cell in the visual cortex of the cat *J Comp Neurol* **241** 111–137

Kratz, K.E., Webb, S.V., Sherman, S.M. (1978a) Electrophysiological classification of X- and Y-cells in the cat's lateral geniculate nucleus *Vis Res* **18** 1261–1264

Kratz, K.E., Webb, S.V., Sherman, S.M. (1978b) Studies of the cat's medial interlaminar nucleus: a subdivision of the dorsal lateral geniculate nucleus *J Comp Neurol* **181** 601–614

Krauth, J. (1983) The interpretation of significance tests for independent and dependent samples *J Neurosci Methods* **9** 269–281

Kruger, J., Fischer, B. (1973) Strong periphery effect in cat retinal ganglion cells: Excitatory responses in ON- and OFF-center neurones to single grid displacements *Exp Brain Res* **18** 316–318

Kuffler, S.W. (1953) Discharge patterns and functional organization of mammalian retina *J Neurophysiol* **16** 37–68

Kulikowski, J.J., Bishop, P.O. (1981) Linear analysis of the responses of simple cells in the cat visual cortex *Exp Brain Res* **44** 386–400

Kulikowski, J.J., Bishop, P.O. (1982) Silent periodic cells in the cat striate cortex *Vis Res* **22** 191–200

Kulikowski, J.J., Bishop, P.O., Kato, H. (1979) Sustained and transient responses

by cat striate cells to stationary flashing light and dark bars. *Brain Res.* **170** 362–367.

Kulikowski, J.J., Bishop, P.O., Kato, H. (1981): Spatial arrangement of responses by cells in the cat visual cortex to light and dark bars and edges. *Exp. Brain Res.* **44** 371–385.

Lee, B.B., Cleland, B.G., Creutzfeldt, O.D. (1977): The retinal input to cells in area 17 of the cat's cortex. *Exp. Brain Res.* **30** 527–538.

Lee, B.B., Elepfandt, A., Virsu, V. (1981): Phase of responses to moving sinusoidal gratings in cells of cat retina and lateral geniculate nucleus. *J. Neurophysiol.* **45** 807–817.

Lee, B.B., Willshaw, D.J. (1978): Responses of the various types of cat retinal ganglion cells to moving contours. *Vis. Res.* **18** 757–765.

Lehmkuhle, S., Kratz, K.E., Mangel, S.C., Sherman, S.M. (1980): Spatial and temporal sensitivity of X- and Y-cells in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* **43** 520–541.

Lennie, P. (1980): Perceptual signs of parallel pathways. *Phil. Trans. R. Soc. Lond.* **B290** 23–37.

LeVay, S. (1973): Synaptic patterns in the visual cortex of the cat and monkey. Electron microscopy of Golgi preparations. *J. Comp. Neurol.* **150** 53–86.

LeVay, S., Ferster, D. (1977): Relay cell classes in the lateral geniculate nucleus of the cat and the effects of visual deprivation. *J. Comp. Neurol.* **172** 563–584.

LeVay, S., Gilbert, C.D. (1976): Laminar patterns of geniculocortical projection in the cat. *Brain Res.* **113** 1–19.

Leventhal, A.G. (1979): Evidence that different classes of relay cells of the cat's lateral geniculate nucleus terminate in different layers of the striate cortex. *Exp.*

Brain Res **37** 349–372

Leventhal A G (1982) Morphology and distribution of retinal ganglion cells projecting to different layers of the dorsal lateral geniculate nucleus in normal and siamese cats *J Neurosci* **2** 1024–1042

Leventhal A G, Hirsch H V B (1978) Receptive-field properties of neurons in different laminae of visual cortex of the cat *J Neurophysiol* **41** 948–962

Leventhal A G, Keens J (1978) Aspects of the topographic organisation of thalamic afferents to cortical areas 17 18 and 19 of the cat *Proc Aust Physiol Pharmacol Soc* **9** 192P

Leventhal A G, Keens J, Tork I (1980) The afferent ganglion cells and cortical projections of the retinal recipient zone (RRZ) of the cat's pulvinar complex *J Comp Neurol* **194** 535–554

Leventhal A G, Schall J D (1983) Structural basis of orientation sensitivity of cat retinal ganglion cells *J Comp Neurol* **220** 465–475

Levick W R, Thibos L N (1980a) Orientation bias of cat retinal ganglion cells *Nature* **286** 389–390

Levick W R, Thibos L N (1980b) X/Y analysis of sluggish-concentric retinal ganglion cells of the cat *Exp Brain Res* **41** A5

Levick W R, Thibos L N (1982) Analysis of orientation bias in cat retina *J Physiol* **329** 243–261

Lin C-S, Friedlander M J, Sherman S M (1979) Morphology of physiologically identified neurons in the visual cortex of the cat *Brain Res* **172** 344–348

Lin C-S, Sherman S M (1978) Effects of early monocular eyelid suture upon development of relay cell classes in the cat's lateral geniculate nucleus *J Comp Neurol* **181** 809–832

Lindstrom, S. (1982): Synaptic organization of inhibitory pathways to principal cells in the lateral geniculate nucleus of the cat. *Brain Res.* **234** 447–453.

Lindstrom, S., Wrobel, A. (1984): Separate inhibitory pathways to X and Y principal cells in the lateral geniculate nucleus of the cat. *Neurosci. Lett. Suppl.* **18** S234.

Livingstone, M., Hubel, D.H. (1981): Effects of sleep and arousal on the processing of visual information in the cat. *Nature* **291** 554–561.

Lund, J., Henry, G.H., MacQueen, C.L., Harvey, A.R. (1979): Anatomical organization of the primary visual cortex (area 17) of the cat. A comparison with area 17 of the macaque monkey. *J. Comp. Neurol.* **184** 599–618.

Maciewicz, R.J. (1975): Thalamic afferents to areas 17, 18 and 19 of cat cortex traced with horseradish peroxidase. *Brain Res.* **84** 308–312.

MacKay, D.M. (1957): Moving visual images produced by regular stationary patterns. *Nature* **180** 849–850.

MacKay, D.M. (1965): Visual noise as a tool of research. *J. Gen. Psychol.* **72** 181–197.

MacKay, D.M., Yates, S.R. (1975): Textured kinetic stimuli for use in visual neurophysiology: an inexpensive and versatile electronic display. *J. Physiol.* **252** 10–11P.

Maffei, L., Fiorentini, A. (1973): The visual cortex as a spatial frequency analyser. *Vis. Res.* **13** 1255–1267.

Magalhães-Castro, H.H., Saraiva, P.E., Magalhães-Castro, B. (1975): Identification of corticotectal cells of the visual cortex of cats by means of horseradish peroxidase. *Brain Res.* **83** 474–479.

Martin, K.A.C. (1984): Neuronal circuits in cat striate cortex. In: Jones, E.G., Peters, A. (eds): *Cerebral cortex. Vol. II. Functional properties of cortical cells.*

Plenum Press, New York. pp241–284

Martin, K A C , Somogyi, P , Whitteridge, D (1983) Physiological and morphological properties of identified basket cells in the cat s visual cortex *Exp Brain Res* **50** 193–200

Martin, K A C , Whitteridge, D (1984) Form, function and intracortical projections of spiny neurones in the striate visual cortex of the cat *J Physiol* **353** 463–504

Mason, C A , Robson, J A (1979) Morphology of retino-geniculate axons in the cat *Neurosci* **4** 79–97

Mason, R (1977) Cell properties in the medial interlaminar nucleus of the cat s lateral geniculate complex in relation to the transient-sustained classification *Exp Brain Res* **22** 327–329

Mason, R (1978a) Neuronal organization within the mammalian dorsal lateral geniculate and adjacent pulvinar nuclei a comparative approach *Ph D Thesis, University of Keele*

Mason, R (1978b) Responses of cells in the dorsal lateral geniculate complex of the cat to textured visual stimuli *Exp Brain Res* **25** 323–329

Mason, R (1978) Functional organization in the cat s pulvinar complex *Exp Brain Res* **31** 51–66

Mason, R (1979) Responsiveness of cells in the cat s superior colliculus to textured visual stimuli *Exp Brain Res* **37** 231–240

Mason, R (1981) Differential responsiveness of cells in the visual zones of the cat s LP-pulvinar complex to visual stimuli *Exp Brain Res* **43** 25–33

Mastronade, D N (1981) Classes of retinal ganglion cells and lateral geniculate cells as functional pathways for visual information *Invest Opthalmol Vis Sci*

Suppl **20** 97

Mastronade, D N (1983) Subtypes of X relay cells in cat LGN can be distinguished solely by responses to visual stimuli *Invest Opthalmol Vis Sci Suppl* **24** 267

Mastronade, D N (1987a) Two classes of single-input X-cells in cat lateral geniculate nucleus I Receptive-field properties and classification of cells *J Neurophysiol* **57** 2 357 380

Mastronade, D N (1987b) Two classes of single-input X-cells in cat lateral geniculate nucleus II Retinal inputs and the generation of receptive-field properties *J Neurophysiol* **57** 2 381 412

Matsubara, J A Cynader, M Swindale, N V (1987a) Anatomical properties and physiological correlates of the intrinsic connections in cat area 18 *J Neurosci* **7** 5 1428 1446

Matsubara, J , Cynader, M Swindale, N V , Stryker, M P (1985) Intrinsic projections within visual cortex evidence for orientation-specific local connections *Proc Natl Acad Sci USA* **82** 935 939

Matsubara, J A , Nance, D M Cynader, M (1987b) Laminar distribution of GABA-immunoreactive neurons and processes in area 18 of the cat *Brain Res Bull* **18** 121 126

Mellwain, J T (1964) Receptive fields of optic tract axons and lateral geniculate cells peripheral extent and barbiturate sensitivity *J Neurophysiol* **27** 1154 1173

Meyer, G , Albus, K (1981a) Spiny stellates as cells of origin of association fibres from area 17 to area 18 in the cat s neocortex *Brain Res* **210** 335 341

Meyer, G , Albus, K (1981b) Topography and cortical projections of morphologically identified neurons in the visual thalamus of the cat *J Comp Neurol* **201**

353-374

Miller, J.W., Buschmann, M.B.T., Benevento, L.A. (1980) Extrageniculate thalamic projections to the primary visual cortex. *Brain Res.* **189**, 221-227.

Mitzdorf, U., Singer, W. (1977) Laminar segregation of afferents to lateral geniculate nucleus of the cat: an analysis of current source density. *J. Neurophysiol.* **40**, 1227-1244.

Mitzdorf, U., Singer, W. (1978) Prominent excitatory pathways in the cat visual cortex (A17 and A18): a current source density analysis of electrically evoked potentials. *Exp. Brain Res.* **33**, 371-394.

Morrone, M.C., Burr, D.C., Maffei, L. (1982) Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. *Proc. R. Soc. Lond.* **B216**, 335-354.

Movshon, J.A. (1981) Functional architecture in the cat's lateral geniculate nucleus. *Invest. Opthalmol. Vis. Sci. suppl.* **20**, 14.

Movshon, J.A., Davis, E.T., Adelson, E.H. (1980) Directional movement selectivity in cortical complex cells. *Soc. Neurosci. Abstr.* **6**, 670.

Movshon, J.A., Thompson, I.D., Tolhurst, D.J. (1978a) Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *J. Physiol.* **283**, 53-77.

Movshon, J.A., Thompson, I.D., Tolhurst, D.J. (1978b) Receptive field organisation of complex cells in the cat's striate cortex. *J. Physiol.* **283**, 79-99.

Movshon, J.A., Thompson, I.D., Tolhurst, D.J. (1978c) Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol.* **283**, 101-120.

Mustari, M.J., Bulher, J., Henry, G.H. (1982) Comparison of response properties of three types of monosynaptic S-cell in cat striate cortex. *J. Neurophysiol.* **47**,

439–454.

Niimi, K., Matsuoka, H., Yamazaki, Y., Matsumoto, H. (1981): Thalamic afferents to the visual cortex in the cat studied by retrograde axonal transport of horseradish peroxidase. *Brain Behav. Evol.* **18** 114–139.

Niimi, K., Sprague, J.M. (1970): Thalamo-cortical organisation of the visual system in the cat. *J. Comp. Neurol.* **138** 219–250.

O'Leary, J.L. (1941): Structure of the area striata of the cat. *J. Comp. Neurol.* **75** 131–164.

Orban, G.A. (1977): Area 18 of the cat: the first step in processing visual movement information. *Perception* **6** 501–511.

Orban, G.A. (1984): *Neuronal operations in the visual cortex. Studies of Brain Function Vol. 11.* Springer-Verlag, Berlin.

Orban, G.A. (1985): Visual cortex and retinal eccentricity: uniformity or non-uniformity. In: Rose, D., Dobson, V.G. (eds): *Models of the visual cortex.* John Wiley and Sons Ltd.

Orban, G.A., Callens, M. (1977a): Receptive field types of area 18 neurones in the cat. *Exp. Brain Res.* **30** 107–123.

Orban, G.A., Callens, M. (1977b): Influence of movement parameters on area 18 neurones in the cat. *Exp. Brain Res.* **30** 125–140.

Orban, G.A., Callens, M., Colle, J.M. (1975): Unit responses to moving stimuli in area 18 of the cat. *Brain Res.* **90** 205–219.

Orban, G.A., Gulyás, B., Vogels, R. (1987): Influence of a moving textured background on direction selectivity of cat striate neurons. *J. Neurophysiol.* **57** 6 1792–1812.

Orban, G.A., Hoffmann, K.-P., Duysens, J. (1985): Velocity selectivity in the cat visual system. I. Responses of LGN cells to moving bar stimuli: A comparison with cortical areas 17 and 18. *J. Neurophysiol.* **54** 1026–1049.

Orban, G.A., Kato, H., Bishop, P.O. (1979a): End-zone region in receptive fields of hypercomplex and other striate neurons in the cat. *J. Neurophysiol.* **42** 818–832.

Orban, G.A., Kato, H., Bishop, P.O. (1979b): Dimensions and properties of end-zone inhibitory areas in receptive fields of hypercomplex cells in cat striate cortex. *J. Neurophysiol.* **42** 833–849.

Orban, G.A., Kennedy, H. (1981): The influence of eccentricity on receptive field types and orientation selectivity in areas 17 and 18 of the cat. *Brain Res.* **208** 203–208.

Orban, G.A., Kennedy, H., Maes, H. (1980): Functional changes across the 17–18 border in the cat. *Exp. Brain Res.* **39** 177–186.

Orban, G.A., Kennedy, H., Maes, H. (1981a): Response to movement of neurons in areas 17 and 18 of the cat: velocity sensitivity. *J. Neurophysiol.* **45** 1043–1058.

Orban, G.A., Kennedy, H., Maes, H. (1981b): Response to movement of neurons in areas 17 and 18 of the cat: directional selectivity. *J. Neurophysiol.* **45** 1059–1073.

Otsuka, R., Hassler, R. (1962): Uber Aufbau und Gliederung der corticalen Sehsphare bei der Katze. *Arch. Psychiatr. Z. Ges. Neurol.* **203** 212–234.

Palmer, L.A., Davis, T.L. (1981): Receptive-field structure in cat striate cortex. *J. Neurophysiol.* **46** 260–276.

Palmer, L.A., Rosenquist, A.C. (1974): Visual receptive fields of single striate cortical units projecting to the superior colliculus in the cat. *Brain Res.* **67** 27–42.

Palmer, L.A., Rosenquist, A.C., Tusa, R. (1975): Visual receptive fields in lamLGNd, MIN, and PN of the cat. *Soc. Neurosci. Abstr.* **1** 54.

Patel, H.H., Sillito, A.M. (1978): Inhibition and velocity tuning in the cat visual cortex. *J. Physiol.* **284** 113–114P.

Peichl, L., Wässle, H. (1979): Size, scatter and coverage of ganglion cell receptive field centres in the cat retina. *J. Physiol.* **291** 117–141.

Peichl, L., Wässle, H. (1981): Morphological identification of on- and off-centre brisk transient (Y) cells in the cat retina. *Proc. R. Soc. Lond.* **B212** 139–156.

Peters, A., Palay, S., Webster, H.D. (1976): *The fine structure of the nervous system: the neurons and supporting cells.* Saunders, Philadelphia.

Peters, A., Regidor, J. (1981): A reassessment of the forms of nonpyramidal neurons in area 17 of cat visual cortex. *J. Comp. Neurol.* **203** 685–716.

Pettigrew, J.D., Nikara, T., Bishop, P.O. (1968): Responses to moving slits by single units in cat striate cortex. *Exp. Brain Res.* **6** 373–390.

Pollen, D.A., Andrews, B.W., Feldon, S.E. (1978): Spatial frequency selectivity of periodic complex cells in the visual cortex of the cat. *Vis. Res.* **18** 665–682.

Raczkowski, D., Rosenquist, A.C. (1981): Retinotopic organization in the cat lateral posterior-pulvinar complex. *Brain Res.* **221** 185–191.

Raczkowski, D., Sherman, S.M. (1985): Morphology and physiology of single neurons in the medial interlaminar nucleus of the cat's lateral geniculate nucleus. *J. Neurosci.* **5** 2702–2718.

Richards, C.D., Webb, A.C. (1975): The effect of nitrous oxide on cats anæsthetized with Brietal. *J. Physiol.* **245** 72–73P.

Riva Sanseverino, E., Galletti, C., Maioli, M.G., Squatrito, S. (1979): Single unit responses to visual stimuli in cat cortical areas 17 and 18. III. Responses to moving stimuli of variable velocity. *Arch. Ital. Biol.* **117** 248–267.

Rockland, K., Lund, J. (1983): Intrinsic laminar lattice connections in primate visual cortex. *J. Comp. Neurol.* **216** 303–318.

Rodieck, R.W. (1965): Quantitative analysis of cat retinal ganglion cell response to visual stimuli. *Vis. Res.* **5** 583–610.

Rodieck, R.W. (1967): Receptive fields of the cat's retina: a new type. *Science* **157** 90–92.

Rose, D. (1977a): Response of single units in cat visual cortex to moving bars of light as a function of bar length. *J. Physiol.* **271** 1–23.

Rose, D. (1977b): On the arithmetic operation performed by inhibitory synapses onto the neuronal soma. *Exp. Brain Res.* **28** 221–223.

Rosenquist, A.C., Edwards, S.B., Palmer, L.A. (1974): An autoradiographic study of the projections of the dorsal lateral geniculate nucleus and the posterior nucleus in the cat. *Brain Res.* **80** 71–93.

Rossignol, S., Colonnier, M. (1971): A light microscope study of degeneration patterns in cat cortex after lesions of the lateral geniculate nucleus. *Vis. Res. Suppl.* **3** 329–338.

Rowe, M.H., Dreher, B. (1979): Perikaryal size of forebrain projecting W-type ganglion cells of the cat's retina. *Proc. Aust. Physiol. Pharmacol. Soc.* **10** 116P.

Rowe, M.H., Dreher, B. (1982): Retinal W-cell projections to the medial interlaminar nucleus of the cat: implications for ganglion cell classification. *J. Comp. Neurol.* **204** 117–133.

Saito, H. (1983a): Morphology of physiologically identified X-, Y-, and W-type retinal ganglion cells of the cat. *J. Comp. Neurol.* **221** 279–288.

Saito, H. (1983b): Pharmacological and morphological differences between X- and Y-type ganglion cells in the cat's retina. *Vis. Res.* **23** 1299–1308.

Sanderson, K.J. (1971): The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. *J. Comp. Neurol.* **143** 101–118.

Sanides, F., Hoffmann, J. (1969): Cyto- and myeloarchitecture of the visual cortex of the cat and of the surrounding integration cortices. *J. Hirnforsch.* **11** 79–104.

Schmielau, F. (1979) Integration of visual and nonvisual information in nucleus reticularis thalami of the cat. In: Freeman, R.D. (Ed): *Developmental Neurobiology of Vision*. Plenum, New York, pp205–226.

Schoppmann, A. (1981): Projections from areas 17 and 18 of the visual cortex to the nucleus of the optic tract. *Brain Res.* **223** 1–17.

Shapley, R.M., Hochstein, S. (1975): Visual spatial summation in two classes of geniculate cells. *Nature* **256** 411–413.

Shapley, R.M., Victor, J.D. (1978): The effect of contrast on the transfer properties of cat retinal ganglion cells. *J. Physiol.* **285** 275–298.

Sherk, H. (1978): Area 18 cell responses in cat during reversible inactivation of area 17. *J. Neurophysiol.* **41** 204–215.

Sherman, S.M., Watkins, D.W., Wilson, J.R. (1976): Further differences in receptive field properties of simple and complex cells in cat striate cortex. *Vis. Res.* **16** 919–927.

Siegel, S. (1956): *Nonparametric statistics for the behavioural sciences*. McGraw-Hill.

Sillito, A.M. (1975): The contribution of inhibitory mechanisms to the receptive field properties of neurones in the striate cortex of the cat. *J. Physiol.* **250** 305–329.

Sillito, A.M. (1977): The spatial extent of excitatory and inhibitory zones in the receptive field of superficial layer hypercomplex cells. *J. Physiol.* **273** 791–803.

Sillito, A.M. (1979) Inhibitory mechanisms influencing complex cell orientation selectivity and their modification at high resting discharge levels. *J. Physiol.* **289** 33–53

Sillito, A.M., Kemp, J.A., Milson, J.A., Berardi, N. (1980b) A re-evaluation of the mechanisms underlying simple cell orientation selectivity. *Brain Res.* **194** 517–520

Sillito, A.M., Kemp, J.A., Patel, H. (1980a) Inhibitory interactions contributing to the ocular dominance of monocularly dominated cells in the normal cat visual cortex. *Exp. Brain Res.* **41** 1–10

Singer, W. (1977) Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiol. Rev.* **57** 386–420

Singer, W., Bedworth, N. (1973) Inhibitory interaction between X and Y units in the cat lateral geniculate nucleus. *Brain Res.* **49** 291–307

Singer, W., Creutzfeldt, O.D. (1970) Reciprocal lateral inhibition of on- and off-center neurones in the lateral geniculate body of the cat. *Exp. Brain Res.* **10** 311–330

Singer, W., Poppel, E., Creutzfeldt, O.D. (1972) Inhibitory interaction in the cat's lateral geniculate nucleus. *Exp. Brain Res.* **14** 210–226

Singer, W., Tretter, F., Cynader, M. (1975) Organization of cat striate cortex: a correlation of receptive field properties with afferent and efferent connections. *J. Neurophysiol.* **38** 1080–1098

Sireteanu, R., Hoffmann, K.-P. (1979) Relative frequency and visual resolution of X- and Y-cells in the LGN of normal and monocularly deprived cats: interlaminar differences. *Exp. Brain Res.* **34** 591–603

Skottun, B.C., Grosof, D., DeValois, R.L. (1985) Responses of simple and complex cells in the cat visual cortex to visual dot stimuli. *Soc. Neurosci. Abstr.* **11** 651

So, Y T., Shapley, R. (1979) Spatial properties of X and Y cells in the lateral geniculate nucleus of the cat and conduction velocities of their inputs. *Exp. Brain Res.* **36**, 533–550.

So, Y T., Shapley, R. (1981) Spatial tuning of cells in and around lateral geniculate nucleus of the cat: X and Y relay cells and perigeniculate interneurons. *J. Neurophysiol.* **45**, 107–120.

Somogyi, P., Kisvarday, Z F., Martin, K A C., Whitteridge, D. (1983) Synaptic connections of morphologically identified and physiologically characterized large basket cells in the striate cortex of the cat. *Neurosci.* **10**, 261–294.

Somogyi, P., Soltész, I. (1986) Immunogold demonstration of GABA in synaptic terminals of intracellularly recorded, horseradish peroxidase-filled basket cells and clutch cells in the cat's visual cortex. *Neurosci.* **19**, 1051–1065.

Soodak, R E., Shapley, R M., Kaplan, E. (1987) Linear mechanism of orientation tuning in the retina and lateral geniculate nucleus of the cat. *J. Neurophysiol.* **58**, 2, 267–275.

Stanford, L R., Friedlander, M J., Sherman, S M. (1980) Morphology of physiologically identified neurons in the C laminae of the cat's lateral geniculate nucleus. *Soc. Neurosci. Abstr.* **6**, 583.

Stanford, L R., Friedlander, M J., Sherman, S M. (1981) Morphology of physiologically identified W-cells in the C laminae of the cat's lateral geniculate nucleus. *J. Neurosci.* **1**, 578–584.

Stanford, L R., Friedlander, M J., Sherman, S M. (1983) Morphological and physiological properties of geniculate W-cells of the cat: a comparison with X- and Y-cells. *J. Neurophysiol.* **50**, 582–608.

Stanford, L R., Sherman, S M. (1983) Morphology of physiologically identified ganglion cells in the cat retina. *Soc. Neurosci. Abstr.* **9**, 884.

Stone, J., Clarke, R. (1980): Correlation between soma size and dendritic morphology in cat retinal ganglion cells: evidence of further variation in the gamma-cell class. *J. Comp. Neurol.* **192** 211–217.

Stone, J., Dreher, B. (1973): Projection of X- and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of visual cortex. *J. Neurophysiol.* **36** 551–567.

Stone, J., Fukuda, Y. (1974): Properties of cat retinal ganglion cells: a comparison of W-cells with X- and Y-cells. *J. Neurophysiol.* **37** 722–748.

Stone, J., Hoffmann, K.-P. (1972): Very slow-conducting ganglion cells in the cat's retina: a major, new functional type? *Brain Res.* **43** 610–616.

Sur, M., Sherman, S.M. (1982a): Retinogeniculate terminations in cats: morphological differences between X and Y cell axons. *Science* **218** 389–391.

Sur, M., Sherman, S.M. (1982b): Linear and nonlinear W-cells in C-laminae of the cat's lateral geniculate nucleus. *J. Neurophysiol.* **47** 869–884.

Suzuki, H. and Ichijo, M. (1967): Tonic inhibition in cat lateral geniculate nucleus maintained by retinal spontaneous discharge. *Jap. J. Physiol.* **17** 599–612.

Symonds, L.L., Rosenquist, A.C. (1984a): Corticocortical connections among visual areas in the cat. *J. Comp. Neurol.* **229** 1–38.

Symonds, L.L., Rosenquist, A.C. (1984b): Laminar origins of visual corticocortical connections in the cat. *J. Comp. Neurol.* **229** 39–47.

Szentágothai, J. (1973): Neuronal and synaptic architecture of the lateral geniculate nucleus. In: Jung, R. (ed): *Handbook of Sensory Physiology, Vol. VII/3B*. Springer-Verlag, Berlin.

Tanaka, K. (1983): Cross-correlation analysis of geniculostriate neuronal relationships in cats. *J. Neurophysiol.* **49** 1303–1318.

Toyama, K., Kimura, M., Shinda, T., Takeda, T. (1977b): Convergence of retinal inputs onto visual cortical cells. II. A study of the cells disynaptically excited from the lateral geniculate body. *Brain Res.* **137**: 221–231

Toyama, K., Kimura, M., Tanaka, K. (1981a): Cross-correlation analysis of interneuronal connectivity in cat visual cortex. *J. Neurophysiol.* **46**: 191–201

Toyama, K., Kimura, M., Tanaka, K. (1981b): Organization of cat visual cortex as investigated by cross-correlation technique. *J. Neurophysiol.* **46**: 202–214

Toyama, K., Maekawa, K., Takeda, T. (1977a): Convergence of retinal inputs onto visual cortical cells. I. A study of the cells monosynaptically excited from the lateral geniculate body. *Brain Res.* **137**: 207–220

Toyama, K., Matsunami, K., Ohno, T., Tokashiki, S. (1974): An intracellular study of neuronal organization in the visual cortex. *Exp. Brain Res.* **21**: 45–66

Tretter, F., Cynader, M., Singer, W. (1975): Cat parastriate cortex: a primary or secondary visual area? *J. Neurophysiol.* **38**: 1099–1113

Troy, J. B. (1983a): Spatial contrast sensitivities of X and Y type neurones in the cat's dorsal lateral geniculate nucleus. *J. Physiol.* **344**: 399–417

Troy, J. B. (1983b): Spatio-temporal interaction in neurones of the cat's dorsal lateral geniculate nucleus. *J. Physiol.* **344**: 419–432

Tso, D. Y., Gilbert, C. D., Wiesel, T. N. (1986): Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *J. Neurosci.* **6**: 1160–1170

Tsumoto, T., Suda, K. (1980): Three groups of cortico-geniculate neurons and their distribution in binocular and monocular segments of cat striate cortex. *J. Comp. Neurol.* **193**: 223–236

Tusa, R. J., Palmer, L. A., Rosenquist, A. C. (1978): The retinotopic organization

of area 17 (striate cortex) in the cat *J. Comp. Neurol.* **177**: 213–236.

Tusa, R. J., Rosenquist, A. C., Palmer, L. A. (1979). Retinotopic organization of areas 18 and 19 in the cat. *J. Comp. Neurol.* **185**: 657–678.

Uchizono, K. (1965). Characteristics of excitatory and inhibitory synapses in the central nervous system of the cat. *Nature* **207**: 642–643.

Updyke, B. V. (1977). Topographic organization of the projections from cortical areas 17, 18 and 19 onto the thalamus, pretectum and superior colliculus in the cat. *J. Comp. Neurol.* **173**: 81–122.

Vakkur, G. J., Bishop, P. O. (1963). The schematic eye in the cat. *Vis. Res.* **3**: 357–381.

Vakkur, G. J., Bishop, P. O., Kozak, W. (1963). Visual optics in the cat, including posterior nodal distance and retinal landmarks. *Vis. Res.* **3**: 289–314.

Victor, J. D., Shapley, R. M. (1979). Receptive field mechanisms of cat X and Y retinal ganglion cells. *J. Gen. Physiol.* **74**: 275–298.

Vidyasagar, T. R., Heide, W. (1986). The role of GABAergic inhibition in the response properties of neurones in cat visual area 18. *Neurosci.* **17**: 49–55.

Vidyasagar, T. R., Urbas, J. V. (1982). Orientation sensitivity of cat LGN neurones with and without inputs from visual cortical areas 17 and 18. *Exp. Brain Res.* **46**: 157–169.

von Grunau, M., Frost, B. J. (1983). Double-opponent-process mechanism underlying RF-structure of directionally specific cells of cat lateral suprasylvian visual area. *Exp. Brain Res.* **49**: 84–92.

Wagner, H.-J., Hoffmann, K.-P., Zwerger, H. (1981). Layer-specific labelling of cat visual cortex after stimulation with visual noise: a [^{3}H]2-deoxy-D-glucose study. *Brain Res.* **224**: 31–43.

Wassle, H., Boycott, B.B., Illing, R.-B. (1981b) Morphology and mosaic of on- and off-beta cells in the cat retina and some functional considerations. *Proc. R. Soc. Lond.* **B212**, 177–197.

Wassle, H., Boycott, B.B. and Peichl, L. (1978) Receptor contacts of horizontal cells in the retina of the domestic cat. *Proc. R. Soc. Lond.* **B203**, 247–267.

Wassle, H., Levick, W.R., Cleland, B.G. (1975) The distribution of the alpha type of ganglion cells in the cat's retina. *J. Comp. Neurol.* **159**, 419–438.

Wassle, H., Peichl, L., Boycott, B.B. (1981a) Morphology and topography of on- and off-alpha cells in the cat retina. *Proc. R. Soc. Lond.* **B212**, 157–175.

Watkins, D.W., Berkley, M.A. (1974) The orientation selectivity of single neurons in cat striate cortex. *Exp. Brain Res.* **19**, 433–446.

Weller, R.E., Humphrey, A.L. (1985) Structural correlates of functional subgroups among X-cells in the cat. *Soc. Neurosci. Abstr.* **11**, 318.

Weyand, T.G., Malpeli, J.G., Lee, C., Schwark, H.D. (1986) Cat area 17. III. Response properties and orientation anisotropies of corticotectal cells. *J. Neurophysiol.* **56**, 1088–1101.

Wilson, M.E. (1968) Cortico-cortical connexions of the cat visual areas. *J. Anat.* **102**, 375–386.

Wilson, M.E., Cragg, B.G. (1967) Projections from the lateral geniculate in the cat and monkey. *J. Anat.* **101**, 677–692.

Wilson, J.R., Friedlander, M.J., Sherman, S.M. (1984) Fine structural morphology of identified X- and Y-cells in the cat's lateral geniculate nucleus. *Proc. R. Soc. Lond.* **B221**, 411–436.

Wilson, J.R., Sherman, S.M. (1976) Receptive-field characteristics of neurons in cat striate cortex: changes with visual field eccentricity. *J. Neurophysiol.* **39**,

512–533.

Wilson, P.D., Rowe, M.H., Stone, J. (1976): Properties of relay cells in cat's lateral geniculate nucleus: a comparison of W-cells with X- and Y-cells. *J. Neurophysiol.* **39** 1193–1209.

Wilson, P.D., Stone, J. (1975): Evidence of W-cell input to the cat's visual cortex via the C-laminae of the lateral geniculate nucleus. *Brain Res.* **92** 427–478.

Wrobel, A., Lindstrom, S. (1984): Mixed X and Y input to principal cells in the lateral geniculate nucleus of the cat. *Neurosci. Lett. Suppl.* **18** S309.