DIRECTIONAL AND ORIENTATIONAL TUNING IN THE STRIATE CORTEX
OF THE CAT FOR CONTRAST AND TEXTURED STIMULI.

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DEDICATION: TO MY PARENTS.

ABSTRACT:

1. Striate cortical neurones respond selectively to the orientation of moving contrast bars. The mechanism for that selectivity has alternatively been attributed to the geniculo-cortical synapse or inhibitory intracortical circuitry. Functionally, that selectivity has suggested a role for the single cell in contour analysis in a hierarchical process of feature extraction.

2. Comparison of tuning of complex cells for moving contrast bars and texture-fields has established the mediation of orientation and direction selectivities by separate mechanisms. An unresolved question is the contributions of orientation and direction to the complex cell's response.

3. Tuning for stationary and moving contrast bars, moving spots and fields of visual noise was evaluated. Tuning for a texture-bar moving across a field of visual noise of similar texture and equal mean luminance was compared with tuning for a moving contrast bar and a field of visual noise.

4. Tuning for a stationary contrast bar had poor predictive value for tuning for moving stimuli; tuning for a stationary bar was sharper and more symmetrical than for the same bar in motion and preferred direction for a spot was not orthogonal to preferred orientation. Preferred direction for texture motion could be predicted from preferred direction for a spot. Cells

bimodal in tuning for a moving texture-field were unimodal in
tuning for a spot. These findings are reviewed in the context of
models for the role of intracortical inhibition.

5. Comparison of tuning for a moving texture-bar with a moving
contrast bar and texture-field demonstrated that, in the
absence of luminance cues, complex cells are sensitive only to
texture motion. A role for direction-selective units in the
representation of form is suggested.

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CHAPTER ONE: THE MODEL OF HUBEL WIESEL
Introduction

A comprehensive model of the striate cortex was proposed
by Hubel and Wiesel (1962, 1963) which incorporated a
description of the stimulus selectivity shown at the single
cell level and an explanatory mechanism for this selectivity
deriving from a comparison of the receptive field organization
at the lateral geniculate and cortical levels. The central
observation initiating this model was the selectivity shown
for the orientation of moving contrast bars. Functionally,
that selectivity was interpreted as defining the role of the
single cell in perception; specifically, neurones in the
visual cortex were conceived as contour detectors. In
essence, the model viewed the transformation of the afferent
input at the geniculo-cortical synapse as the means by which
the striate cortex derived its stimulus selectivity. The
function of that mechanism was to ensure the selective
response to luminance contours in a hierarchical process of
feature analysis within the cortex.

On the basis of receptive field organization, striate
cortical cells were classified into three groups, each of
which exhibited the property of orientation selectivity but
with varying degrees of precision and requirements for
restriction in the dimensions of the stimulus. Moreover, the
various categories of neurone so defined were viewed as acting
in unison; they contributed to the same circuitry and formed
a functional unit. The cortical sheet was conceived as being
divided into columns each containing the three categories of

neurone, in a serial chain, and in an invariant order. The difference between these units lay in the particular orientation preference shown by each column, the identity of each being the shared common orientation preference. The work of Hubel and Wiesel revised the concept of the visual cortex as a structure with myriads of cells taking part in the formation of every visual image; each cell was found to have specific stimulus requirements and the cortex was divided into functional units with equally clearly defined stimulus requirements.

Both the origin and functional significance of the selectivity for oriented moving contrast bars have been conjectural. The question of mechanism will be raised at this stage. The central role of the afferent input in determining stimulus selectivity at the cortical level has been brought into doubt by empirical tests of the assumption of convergence of afferent fibres (Creutzfeldt and Ito, 1968; Creutzfeldt, Kuhnt and Benevento, 1974; Lee, Cleland and Creutzfeldt, 1977; Sillito, Kemp, Milson and Berardi, 1980; Berardi, Kemp, Milson and Sillito, 1980), from consideration of the relationship between the simple cell receptive field plotted with flashed bars and the contribution of the afferent input from the lateral geniculate nucleus (Creutzfeldt, Kuhnt and Benevento, 1974; Sillito 1975; Berardi, Kemp, Milson and Sillito, 1980), and the predictability of response from the receptive field plotted in this way (Henry and Bishop, 1972; Bishop, Dreher and Henry, 1972; Henry, Bishop and Dreher, 1974; Henry, Dreher and Bishop, 1974; Watkins and Sherman, 1974; Goodwin, Henry and Bishop, 1975; Nothdurft, 1976;

Schiller, Finlay and Volman, 1976a; Henry, 1977). An alternative proposal is that orientational/directional selectivity is mediated by intracortical processes of a predominantly inhibitory nature (Benevento, Creutzfeldt and Kuhnt, 1972, Creutzfeldt, Kuhnt and Benevento, 1974; Sillito, 1976). Evidence will be presented to support this contention.

Orientation selectivity was assessed with moving contrast bars in Hubel and Wiesel's original work and orientation was not dissociated from direction. Whilst subsequent studies have yielded some insight of separate contributions of orientation and direction using this stimulus paradigm, particularly in the context of intracellular recordings (Creutzfeldt, Kuhnt and Benevento, 1974; Innocenti and Fiore, 1974) and blocking of intracortical inhibition (Sillito, 1974, 1975, 1976, 1977; Tsumoto, Eckart, and Creutzfeldt, 1979), the contribution of these two parameters was left unanswered in Hubel and Wiesel's studies. A specific proposal that separate mechanisms operate intracortically to generate orientation and direction selectivities (Schiller, Finlay and Volman, 1976; Hammond, 1978) has considerable support from comparisons of tuning for contrast and textured stimuli (Hammond, 1978; Hammond and Reck, 1980a, b; Hammond, 1981b). This and related evidence will be presented.

A model in which orientational and directional selectivities are determined by separate mechanisms involving intracortical inhibition forms the background to the research to be described. In this theoretical context the question is raised of the contribution of these separate mechanisms to the

cell's response and it is to this question that the research
presented here is addressed. Summatory requirements for
effective drive for many cortical neurones precludes answering
the question with contrast stimuli alone. Moving fields of
texture, in particular visual noise (Hammond and Mackay, 1975a
and subsequently), provide a stimulus with directional drive
free from orientation and at the same time fulfilling
summatory requirements. The differential responsiveness of
cortical units to visual noise (Hammond and Mackay, 1975a,b;
1976; 1977) restricts the study to one category of neurone,
the complex cell of Hubel and Wiesel's classification (Hubel
and Wiesel, 1962). A paradigm employing a combination of
contrast and visual noise stimuli provides a means of
investigating the contributions of orientation and direction
mechanisms determining the complex cell's response.

Several stages of discussion precede the presentation of
the current research. The first of these centres on the model
of Hubel and Wiesel, important not only for the mechanism it
proposed for orientational selectivity, but also for its
wide-ranging propositions concerning the organization of the
striate cortex, the classification of cortical units and their
inter-relationships. Subsequent models are derived from
consideration of the many aspects of Hubel and Wiesel's model.

1.1 An Outline of Hubel and Wiesel's Model

Hubel and Wiesel's (1962) comparison of response
specificities of visual cortical and lateral geniculate
neurones revealed that the receptive field of lateral

geniculate neurones, responding to flashed spots with a circular centre-surround organization, gave way to elongated receptive fields responsive to moving oriented lines and borders at the cortical level. In the   the simple cell, the neurone presumed to occu. .ne first ordinal position from the geniculate input to the cortex, the receptive field was found to be divided into separate regions, parallel to the orientation axis, responding to opposite polarities of flashed contrast bars.   It was argued that orientation and direction selectivity could be understood from the disposition of these regions which in turn reflected the spatial arrangement of the afferent input. Orientational selectivity was derived from the principle of summation within, and antagonism between, these areas. Formation of the simple cell receptive field by convergence of fibres, representing aligned receptive fields of lateral geniculate neurones resulted in the sub-regions of the simple cell receptive field. In illustration, an "on-centre" LGN neurone group would give rise to a simple cell with a central region responding to a bright bar flanked by two regions responding to a dark bar. Such a simple cell became the paradigm for simple cell models (Hubel and Wiesel, 1962, 1963, 1968). The receptive field centres of geniculate neurones were considered to lie in a straight line and extending the length of the stimulus, of appropriate contrast, would cause an increased response as more geniculate field centres were stimulated. Antagonism (or inhibition as Hubel and Wiesel sometimes referred to it) between regions would cause a reduction and eventual elimination of response as the stimulus deviated from the "orientation axis" and encroached into the antagonistic

zones. Such antagonism between zones of LGN cells, it was argued, would result in the withdrawal of excitation to the cortical cells and decreased response. Each simple cell was considered to receive convergent input from either "on"- or "off"-centre fibres. However, Hubel and Wiesel (1962) raised the possibility of enlargement and reinforcement of the inhibitory flanks of the receptive field by "off"-centre geniculate fibres (in the case of "on"-centre simple cells) or "on"-centre geniculate fibres (in the case of "off" centre simple cells).

The lack of a clear division into antagonistic regions within the receptive field and the absence of summation within each region for a second category of cell, the complex cell, implied that these neurones could not receive direct input from the lateral geniculate nucleus. But, the authors argued, the receptive field of this type of neurone is compatible with convergent input from several simple cells stepped in position with the same orientation axis but sequentially different retinal locations. Finally, a third category of neurone, the hypercomplex cell, assumed to be formed by the convergence of several complex cells, exhibits the property of end-inhibition, conferring upon it a selectivity for bars restricted in length.

The three categories of cells were conceived as being linked by excitatory connections in a serial chain from the afferent input; simple, complex, hypercomplex. Such a serial chain comprised an orientation column, tuned by the afferent input and segregated from synaptic contact with members of the

adjacent column. So described, the column forms an anatomical and functional entity. Hubel and Wiesel did not, however, entirely rule out interactions between adjacent columns in the limited case of the formation of the large receptive fields of exceptional complex cells, though such occurrences were considered infrequent and a hierarchical organization of neurones was still complied with.

Economy of wiring required that orientation columns with similar orientations were close together. Such an organization would be discernible through the successive steps in preferred orientation when recorded by an electrode tangentially coursing through the cortex. In some parts of the cortex columns were found to be arranged in a very regular manner. For these cases discrete shifts in orientation would be evident in recordings from a tangentially advanced electrode. In these ordered regions the columns are especially likely to be long and narrow. For other parts of the cortex, Hubel and Wiesel found little order in the arrangement of neighbouring columns. In some cases, "columns" were found to take the form of "slabs" and, in the monkey, the representation was found to be more compatible with a continuous rather than discrete representation of orientation (Hubel and Wiesel,1974). The columnar organization apparent in physiological recordings was not matched by an anatomical substrate of predictable dimensions and shape.

Specific proposals relate to the various elements of Hubel and Wiesel's model; the role of the afferent input, the classification of cortical neurones in relation to the

afferent input, the relationships between these neurones within the cortex, and the vertical segregation of these types into functional units with common response specificities. Each of these aspects of the model is considered.

1.2 The Role of the Afferent Input in Hubel and Wiesel's Model

The afferent input was assumed to be homogeneous in type, limited in distribution, and untuned in terms of showing no selectivity in response to oriented moving bars. The most important assumption in relation to the geniculate input is that fibres converge onto the simple cell in an aligned manner.

Hubel and Wiesel's (1962) model assumed the predominant site of termination of afferent fibre input to be lamina IV, with a lesser distribution to lamina VI. Such a distribution had been reported by Nauta (1954) and has since been confirmed by numerous studies (e.g. Wilson and Cragg, 1967; Colonnier and Rossignol, 1969; Hubel and Wiesel, 1969; Garey, 1970). However, the distribution of thalamo-cortical fibres has subsequently been found to show a more complex pattern of laminar distribution. This pattern of distribution is not simply numerically greater, in terms of laminae contacted, but represents a pattern of distribution specifically related to different types of afferent fibres. Such fibres represent parallel streams running from retina to cortex (Wilson and Cragg, 1967; Cleland, Dubin and Levick, 1971; Hoffmann, Stone, and Sherman, 1972; Stone and Dreher, 1973; Sherman, Norton and Casagrande, 1975; Tretter, Cynader and Singer,

1975; Wilson and Stone, 1975; Cleland, Levick, Morstyn and
Wagner, 1976; Hale, Dreher and Leventhal, 1978).

Three categories of retinal ganglion cell, showing
differences in morphology, distribution and conduction
velocities have been described (Enroth-Cugell and Robson,
1966; Bishop, Clare and Landau, 1969; Cleland, Dubin and
Levick, 1971; Cleland, Levick and Sanderson, 1973; Cleland
and Levick, 1974a, b; Stone and Hoffmann, 1972; Fukuda and
Stone, 1974, 1975; Stone and Fukuda, 1974a, b; Rowe and
Stone, 1976) referred to as X, Y and W cells, or sustained,
transient, and sluggish and non-concentric cells. The X cell
is characterised by a medium sized soma, small dendritic and
receptive fields (Enroth-Cugell and Robson, 1966; Boycott and
Wassle, 1974; Cleland and Levick, 1974a, b; Fukuda and Stone
1974, 1975; Hammond, 1974; Stone and Fukuda, 1974a, b;
Levick, 1975). This type of cell is concentrated around the
area centralis and projects to the cortex via the A laminae of
the dorsal lateral geniculate nucleus (Wilson and Cragg, 1967;
Cleland, Dubin and Levick, 1971; Hoffmann, Stone and Sherman,
1972; Wilson, Rowe and Stone, 1976; Dreher and Sefton,
1979). In contrast, the Y cells have large soma, large
dendritic and receptive fields and thick, fast conducting
axons (Enroth-Cugell and Robson, 1966; Bishop, Clare and
Landau, 1969; Cleland, Dubin and Levick, 1971; Boycott and
Wassle, 1974; Cleland and Levick, 1974; Fukuda and Stone,
1974, 1975; Hammond, 1974; Stone and Fukuda, 1974; Levick,
1975). Compared with X cells they are relatively greater in
number in the peripheral retina but as a category congregate
in the area centralis and the visual streak (Enroth-Cugell and

Robson, 1966; Cleland, Levick and Sanderson, 1973; Fukuda
and Stone, 1974; Rowe and Stone, 1976). These cells project
to the cortex via the A and C laminae of the LGNd (dorsal
Lateral Geniculate Nucleus) and also the MIN (Medial
Interlaminar Nucleus) (Wilson and Cragg, 1967; Cleland, Dubin
and Levick, 1971; Hoffmann, Stone and Sherman, 1972; Wilson,
Rowe and Stone, 1976; Mason, 1976; Dreher and Sefton, 1979).
W cells form a population of small to medium sized ganglion
cells with thin, slow conducting axons and large dendritic and
receptive fields (Stone and Hoffmann, 1972, Cleland and
Levick, 1974a; Stone and Fukuda, 1974; Fukuda and Stone,
1975; Levick, 1975). Concentrated in the visual streak and
area centralis (Fukuda and Stone, 1974), they form 50-55% of
all ganglion cells. The relay to the cortex of these cells is
via the parvocellular C laminae of LGNd (Wilson and Cragg,
1967; Hoffmann, Stone and Sherman, 1972; Cleland, Levick,
Morstyn and Wagner, 1976; Wilson, Rowe and Stone, 1976;
Dreher and Sefton, 1979) and MIN (Dreher and Sefton, 1979;
Mason and Robson, 1979; Guillery, Geisert, Polley and Mason,
1980; Rowe and Dreher, 1982).

The distribution of these three types of fibres differs
between cortical areas and in laminar distribution within a
specific area. The striate cortex is the site of projection
of X fibre input from the LGN (Hoffmann and Stone, 1971;
Stone and Dreher, 1973; Singer, Tretter and Cynader, 1975;
Dreher, Hale and Leventhal, 1978), but both Y and W cells also
provide input to area 17 (Singer, Tretter and Cynader, 1975;
Ferster and LeVay, 1978; Leventhal, 1979). In the striate
cortex, the three categories show the following pattern of

laminar projection; X cells project to laminae IVc and VI; Y cells project to laminae IVab and VI; W cells project to layers I, III and the layer IV-V border area (Singer, Tretter and Cynader, 1975; Tretter, Cynader and Singer, 1975; Ferster and LeVay, 1978; Leventhal, 1979).

The consequences of this distribution in the present context are: firstly, the distribution of fibres is such that, with the exception of lamina II, each of the laminae of the cortex acts as a recipient site for the afferent fibres; secondly, that such a segregation pattern of fibre terminations may represent separate pathways, certainly at the first synapse, and potentially beyond the first synapse. Recent evidence supports the second possibility (Bullier and Henry, 1979b; Mustari, Bullier and Henry, 1982). The distribution of cells in laminae away from the principal lamina of termination of fibres, lamina IV, does not therefore preclude their occupying the first ordinal position in the cortex as suggested in Hubel and Wiesel's work. To the extent that such parallel streams remain segregated to the point of the geniculo-cortical synapse, the laminar distribution of cell types (Gilbert, 1977; Leventhal and Hirsch, 1978; Bullier and Henry, 1979), raises the possibility that different cell types receive different afferent inputs (Stone and Dreher, 1973; Hoffmann and Stone, 1971; Dreher, Hale and Leventhal, 1978). Even if not segregated in terms of specific correspondence of fibre type and cell type contacted, processing of these separate parallel streams may continue through the cortex, both complicating and contradicting the serial processing envisaged by Hubel and Wiesel.

Several studies have shown that, contrary to the initial report of Hubel and Wiesel (Hubel and Wiesel, 1962), the LGN does show some degree of orientational tuning when tested with moving bars (Daniels, Norman and Pettigrew 1977; Creutzfeldt and Nothdurft, 1978; Lee, Creutzfeldt and Elepfandt, 1979; Vidyasagar and Urbas, 1982). Of the two alternative possibilities for the origins of this bias, namely the geniculate suppressive field (Levick, Cleland and Dubin, 1972) or the asymmetries seen in retinal ganglion cell receptive fields (Hammond, 1974; Levick and Thibos, 1980) the mechanism was attributed by Vidyasagar and Urbas (1982) to the suppressive field but with some retinal contribution. This study revealed strong orientation biases in the LGNd for the vertical and horizontal orientations; oblique orientations are first represented in the cortex. An interesting possibility raised by these authors is the role of the afferent input from the geniculate in forming two principal co-ordinates from which the cortex generates other orientations, a proposition deriving from the theoretical model of Von der Malsberg (1973) and Von der Malsberg and Cowan (1982). Essentially though, this proposition is speculative. The main point raised by this and the preceding studies is that orientation tuning cannot be seen as an exclusively cortical phenomenon though undoubtedly it reaches greater prominence and functional significance at that level (Creutzfeldt and Nothdurft, 1978).

The consideration of the relationship between the afferent input and the simple cell first requires a description and evaluation of Hubel and Wiesel's

classificatory system.

1.3 The Classificatory System of Hubel and Wiesel

Three broad questions are raised by Hubel and Wiesel's classificatory system. The first concerns the empirical validity and comprehensiveness of that scheme; can three categories of neurone be distinguished by their criteria and can the system account for all the diverse receptive field types? The second is the extent to which the classificatory system may be used for predicting the ordinal position of neurones in a serial chain. Thirdly, the question is raised of the relationship between the classes of cells defined by receptive field organization and the categories of neurone defined by morphological criteria, and the extent to which a knowledge of this correlation might reveal the functional significance of the various morphological types.

The defining criteria of the various categories of neurone in Hubel and Wiesel's scheme may be summarized as follows. Simple cells exhibit the following properties.

(1) The receptive field, plotted with stationary flashed stimuli of appropriate contrast, has separate elongated "on" and "off" regions.

(2) In common with retinal ganglion and lateral geniculate receptive fields, simple cell fields show summation of responses within an "on" or "off" region and antagonism between "on" and "off" regions. However, Henry (1977) has pointed out that summation of response was originally reported for circular spot stimuli increasing in size. Since Hubel and

Wiesel later evaluated summation with elongated bars and summation of response along the "orientation axis" is exhibited by both simple and some complex cells, summation of response orthogonal to optimal orientation must be the property exclusive to simple cells.

(3) The orientation selectivity of simple cells, and to a lesser extent the directional selectivity as well, can be explained by and predicted from the layout of the "on" and "off" areas.

Complex cells exhibit the following characteristics;

(1) "On" and "off" areas of the receptive field are often not separate. In most cases flashing stimuli evoke on-off responses or no response.

(2) Where separate "on" and "off" areas can be distinguished in the receptive field, summation within and antagonism between these separate regions is not found.

(3) Complex cells show an orientation selectivity which is position independent; the cells are sensitive to the preferred orientation over a range of positions in the receptive field.

(4) The responses of complex cells to moving objects can neither be predicted nor explained from the maps of the receptive field made with small spots.

(5) Complex cells are only rarely encountered in layer IV of the cortex, the major site of termination of geniculo-cortical axons.

Hypercomplex cells are defined in the following way;

(1) The cells are located in layers of the cortex away from the major termination site of geniculo-cortical afferents.

(2) They exhibit a property of end-inhibition, making them

selective not only for the orientation of the stimulus but also its length. Importantly, the end-inhibition is seen as an all-or-none phenomenon displayed by a distinct group of cells and not a varying property shown by different classes (i.e. simple and complex cells).

(3) The end-zone inhibition is orientation sensitive, being generated by a lower level orientation-selective cell, presumed to be the complex cell.

(4) The hypercomplex cell is found less frequently in area 17 and increasingly in areas 18 and 19, areas assumed in Hubel and Wiesel's model to be in a hierarchical relationship to area 17, and at a higher step in the hierarchy.

Contrary to the early reports of Hubel and Wiesel, a number of studies have reported hypercomplex cells to be present in striate cortex, distributed in laminae II, III and V. (Camarda and Rizzolatti, 1976; Camisa, Blake and Lane, 1977; Palmer and Rosenquist, 1974; Gilbert, 1977; Rose, 1977; Kato, Bishop and Orban, 1978; Leventhal and Hirsch, 1978). Also, Hubel and Wiesel (1968) reported hypercomplex cells being common in both cat and monkey striate cortex, reversing their earlier view.

The cells in area 17 which exhibit end-inhibition do not constitute a separate group however. There is now substantial evidence that the property of end-inhibition is not the attribute of a separate and distinct group of neurones and, more specifically, it is not an all-or-none phenomenon. Dreher (1972) reported that both simple and complex cells can exhibit end-inhibition and this has subsequently been

confirmed by Carmarda and Rizzoletti (1976), Wilson and
Sherman (1976), Hammond and Andrews (1978a, b), Leventhal and
Hirsch (1978), and Orban, Kato and Bishop (1979). Though
Kato, Bishop and Orban, (1978) reported that they could
identify cells which were hypercomplex but not simple or
complex in receptive field organization, cells with simple or
complex properties with end-inhibition were found. Moreover,
Rose (1977) demonstrated that end-inhibition is not an all or
none phenomenon. This gradation of inhibition has been
reported by Wilson and Sherman (1976) and Gilbert (1977). In
summary, end-inhibition is a varied attribute of some simple
and complex cells.

The question of two distinct cell types, simple and
complex, is more problematical, not least because of the
logical grounds for classifying in Hubel and Wiesel's scheme.
Simple and hypercomplex cells are defined by attribution,
complex cells by exclusion. In other words, both the simple
and the hypercomplex cells are defined by possession of
certain attributes – in the case of simple cells, separation
of the receptive field into zones with properties of summation
and antagonism; in the case of hypercomplex cells, the
presence of end-inhibition. On purely logical grounds,
therefore, such a grouping would most likely be
non-homogeneous.

Within the classificatory framework of Hubel and Wiesel,
several sub-groups of complex cell have been defined. Henry
(1977) has referred to three classes of complex cell.
Approximately fifty-five per cent of these comprise cells with

a receptive field of mixed on/off discharge, the remaining forty-five per cent being divided between two sub-classes. The first has a non-uniform receptive field with distinct areas of on and off discharge, being distinct from the simple cell by the failure to show summation of response orthogonal to preferred orientation. The other, and least common complex cell, is unresponsive to flashed light bars or spots but is discharged by exposure to a stationary edge or bar of optimal orientation positioned at any point in the receptive field. Of the three, only the uniform-field complex cell is found in appreciable numbers in the cat striate cortex (Henry, 1977).

Gilbert (1977) has divided complex cells into two groups according to their summatory behaviour along the orientation axis. "Standard" complex cells exhibit summation of response with increased bar length whilst "Special" complex show similar magnitude of response for spot stimuli and for extended bars. Standard complex cells are distributed in laminae II and III (small to intermediate field sizes), lamina V (with intermediate field sizes) and lamina VI (with large receptive field sizes). Special complex cells are reported to be present in lamina V (Palmer and Rosenquist, 1974, Gilbert, 1977) and lamina III (Gilbert, 1977). Special complex cells are absent from and Standard complex cells scarce in lamina IV (Gilbert, 1977).

Henry (1977) and Henry, Lund and Harvey (1978) have identified a complex cell which they refer to as a B cell. In summatory behaviour a "Standard" complex cell, the B cell is distinguished from other complex cells by its generally small

receptive field (less than two degrees in length and width), preferring slow velocities of stimulus movement and showing little or no spontaneous activity and a sustained response to bar flash. Distributed in laminae II and III, including the III/IV border, and lamina Va, B cells form the predominant source of projection to the Clare-Bishop area (Henry, Lund and Harvey, 1978).

Without assuming homogeneity within each group, the evidence would suggest that a separation between simple and complex groups can be achieved by the criterion of the segregation of the receptive field into zones but the picture relating to summatory behaviour is less clear cut. Many studies have verified the separation of simple and complex categories by the presence or absence of divisions within the receptive field (Maffei and Fiorentini, 1973; Toyama, Maekawa and Takeda, 1973; Kelly and Van Essen, 1974; Drager, 1975; Goodwin and Henry, 1975; Ikeda and Wright, 1975; Movshon, 1975; Singer, Tretter and Cynader, 1975; Camarda and Rizzoletti, 1976; Hammond and Andrews, 1978a, b, c). The problem of summatory behaviour relates to the conditions under which the summation is tested and the dimension in which summation is assessed. Henry (1977) has pointed out not only that summation orthogonal to the orientation axis is peculiar to simple cells but that this difference in summatory behaviour is only evident under threshold conditions. On grounds of receptive field division but not summatory behaviour the classificatory system is robust.

An important specification about the type of cell

contacted by the afferent input was made in the model - only
simple cells were the recipients of direct afferent input.
Because only these cells were recorded from the principal
layer of afferent fibre termination, the fourth layer, a
unique relationship between afferent fibres and cells of this
type was assumed, the basis of the assumption being that
geniculate fibres contact cell bodies. Only those cells whose
cell bodies are located in lamina IV would therefore be the
recipients of direct afferent input. Anatomical studies have
demonstrated that afferent fibres make contact with cell
dendrites (Garey and Powell, 1971; Winfield and Powell, 1976)
and that dendrites of pyramidal cells extend out of layers in
which the cell body is located to layers of afferent fibre
termination (Cajal, 1911, 1922; O'Leary, 1941; Lorente de
No, 1949; Lund, Henry and Harvey, 1979). Therefore, those
cells located outside the principal lamina of afferent fibre
termination can receive direct monosynaptic input.

The correlation between the laminae of termination of
afferent fibres and cell types based on receptive field
organization seemed to parallel the distribution of two
morphological types; the spiny stellate and pyramidal cells.
The main difference between these lies in the possession of a
prominent apical dendrite by the pyramidal cell. It had been
known that spiny stellate cells are distributed in the major
lamina of afferent fibre termination and that pyramidal cells
lie outside that lamina (Cajal, 1922; Lorente de No, 1922;
O'Leary, 1941). The correlation between spiny stellate cells
and simple cells, and complex cells and pyramidal cells
reported by Kelly and Van Essen (1974) appeared to provide the

basis for assigning roles to morphologically defined types. That correlation was not however perfect, some pyramidal cells with simple cell receptive fields being amongst their sample. A simple equation of cell types defined by receptive field structure and morphological criteria has not been fulfilled and no single morphological type is seen to be the exclusive recipient of geniculate fibre input. Simple cells are represented by both spiny stellate and pyramidal neurones. Whether a pyramidal cell exhibits simple cell receptive field structure or not appears to depend on the proximity of the basal dendrites to the afferent input (Wiesel and Gilbert, 1981). In contrast to the diverse morphological types having simple cell receptive field structure, the three studies pertinent to the point (Kelly and Van Essen, 1974; Lin, Friendlander and Sherman, 1979; Wiesel and Gilbert, 1981) indicate a high correlation between the complex category and the pyramidal neurone.

1.4. The Interrelationships of Cells in Hubel and Wiesel's Model

The question of the interrelationships between cells in Hubel and Wiesel's model arises in two contexts; the relationships between cell types based on classification by receptive field organization and the interrelationships between cells of the same orientation column. Of course, these are two aspects of the same problem but the special features and importance of the columnar concept in the model warrant separate consideration.

Linkages between cells were considered to be excitatory, one-directional and hierarchical, from simple to complex to hypercomplex. It has already been argued that the hypercomplex category does not represent a separate category of neurone. Evidence will now be presented to counter the suggestion that the complex cell is invariably a second order cortical neurone. The sources of this view are twofold: (1) from latency studies; (2) from evidence that complex cells respond to a range of stimuli to which simple cells are unresponsive.

An early study by Denny, Baumgartner and Adorjani (1968) indicated that all complex cells have latencies reflecting a second order position in relation to the geniculate input to the cortex. Subsequent studies, in which latencies to electrical stimuli were measured for cells identified by their receptive field organization, have established that some proportion of complex cells can be first order cortical neurones (Hoffmann and Stone, 1971; Stone, 1972; Stone and Dreher, 1973; Toyama, Maekawa and Takeda, 1973, 1977; Bullier, Harvey and Henry, 1978). Secondly, comparing the velocity selectivity of simple and complex cells, Movshon (1975) found that some complex cells respond to moving bars at velocities outside the range to which simple cells respond. Thirdly, it was established by Hammond and MacKay (1975a) and confirmed by subsequent studies (e.g. Hammond and Mackay, 1975b, 1976, 1977; Hoffmann and von Seelen, 1978, in the striate cortex and Dinse and von Seelen, 1978 in extrastriate cortex) that complex cells but not simple cells respond to texture motion and that simple cells are therefore not the

sole input to complex cells.

A situation in which complex cells may be first order cortical neurones, receiving direct afferent input from the LGN, does not lead to a complete refutation of the suggested relationship between simple and complex neurones, particularly in the light of evidence that a proportion of complex cells has been shown to receive an orientationally tuned input (Sillito, 1976), from evidence that some complex cells have latencies to electrical stimulation consistent with their being second order cortical neurones (eg. Denny, Baumgartner and Adorjani, 1968; Bullier, Harvey and Henry, 1978), and that some complex cells receiving direct LGN input receive additional intracortical inputs (Singer, Tretter and Cynader, 1975; Bullier and Henry, 1979a). Clearly, the serial sequence suggested by Hubel and Wiesel can only be part of the story since simple cells may provide only some of the attributed input to some complex cells. Indeed, the picture is further complicated by recent evidence that inhibitory influences - acting in reverse order to the proposed hierarchy - exist, since moving fields of visual noise, to which simple cells are unresponsive, have been found to influence their response to moving contrast bars (Hammond and Mackay, 1978, 1981). The question of the interrelationships of simple and complex cells will be returned to. The conclusion at this stage is that complex cells do not receive an exclusive simple cell input, that within the complex cell group a diversity of connectivity patterns exists, and that all complex cells exhibit properties which cannot be derived from a simple cell input.

1.5. The Columnar Concept and its Empirical Validity

The concept of the orientation column is central to Hubel and Wiesel's model in explaining the response specificity of second and third order cortical neurones. Though the concept of the orientation column has subsequently been modified (Hubel and Wiesel, 1962, 1972, 1977), it implies the striate cortex is sub-divided into discrete regions or columns extending from the surface to the white matter in which all cells common to the column have the same "receptive field axis orientation" (Hubel and Wiesel, 1962), i.e. it is defined in terms of common response specificities of a group of neurones in vertical proximity. The question of the shape of such columns or slabs (Hubel and Wiesel, 1977) is secondary to that of an anatomical and functional segregation of cells within a cortical area. Without making presuppositions about the shape of these cell aggregates, two requirements are necessary for the concept to acquire empirical validity; that the column is a discrete entity definable by anatomical criteria, and that vertical interactions within a column can be demonstrated. Though inhibitory connections could play some role in the formation of a column, the specific requirement in the model is that of excitatory connections as described previously. Creutzfeldt, Innocenti and Brooks (1974) have argued against the formation of an orientation column by inhibitory connections on the basis that members of the same column differ in the spatial extents of the inhibitory components of their receptive fields. The equation of the inhibitory zones described in Creutzfeldt, Innocenti and Brooks (1974) with those mediating orientation tuning is not, however,

self-evident.

The evidence brought forward in support of the concept of an orientation column is the following.

(1) Penetrations perpendicular to the surface reveal cells whose response retains the same orientation preference (Hubel and Wiesel, 1962, 1972, 1977).

(2) In oblique penetrations, graphs of orientation plotted against track distance are straight lines through the cortical thickness (interrupted in part through layer IVc of the monkey in which non-oriented cells are present) (Hubel and Wiesel, 1974).

(3) In tangential penetrations abrupt shifts in preferred orientation are encountered (Hubel and Wiesel, 1974).

(4) Using the de-oxyglucose method of Sokoloff (1977) as an index of cellular activity, tangential sections following selective monocular exposure to single orientations reveal columns perpendicular to the surface.(Stryker, Hubel and Wiesel, 1977; Hubel, Wiesel and Stryker, 1978).

Though demonstrated by physiological techniques and defined in functional terms, implicit in the concept of the orientation column is an anatomical substrate, and herein lies the difficulty. The problem is summarized by Gould and Ebner (1977).

"It has not been possible, however, to provide a precise anatomical definition of a column boundary in the visual cortex based on the anatomical characteristics of functionally related groups of neurones. The problem lies in the concept

of the 'boundary' itself and in the problem of determining the
features of an anatomical boundary. If a boundary for a
cortical column is set, it implies a type of anatomical
discreteness between adjacent groups of cortical cells or that
some different type of cellular organization lies beyond the
boundary or set of columns, for example, or the border of a
set of columns, or the border between two cytoarchitectural
areas. Because columns may overlap and be of variable size
and shape, it may prove difficult to demonstrate anatomical
discreteness of vertical columns with the usual anatomical
techniques."

The pattern of connectivity forming a column, though
requiring a discontinuity of intracortical connectivity at the
columnar boundary, would only require a partial segregation of
the afferent input between columns. Within a column an
oriented group of fibres from the LGN confers upon the column
a particular orientation. A given system of fibre groups
would be appropriate only to cells with a particular receptive
field orientation. Therefore, some of the fibres making up a
bundle would change at each columnar boundary, this change
leading to a progression of preferred orientation. However,
Hubel and Wiesel themselves (1974) noted the lack of agreement
between columnar width and receptive field dimensions of
afferent fibres, Lund (1981b) reported no agreement between
columnar and basal dendrite width in any lamina and in a
review of the problem Szentagothai (1975) could identify no
boundary feature of a column.

In considering the evidence for the discreteness of

orientation columns it becomes important to emphasize the paradigm in which such discreteness was revealed. The experimental approach of Hubel and Wiesel (1962, 1972, 1977) was to make _limited_ measurements of _preferred_ orientation for a moving bar in penetrations perpendicular and tangential to the cortical surface. Such a paradigm confers upon the members of a column a greater specificity for orientation than might be revealed by measurements of the range of orientations to which a cell is responsive and might lead to a picture in which columns respond in an all-or-none manner (i.e. for a particular bar orientation this would lead to either a response of all members in unison, or no response; there is no room in the model for non-optimal orientation resulting in sub-maximal firing).

Two strategies have been adopted to investigate the validity of the concept of the orientation column since the initial studies of Hubel and Wiesel. Firstly, a group of experiments which in outline replicate Hubel and Wiesel's pioneering studies but additionally consider breadth of tuning as well as optimal orientation preference, and a second group of experiments which look at the correlation of activity of cells within a column to investigate directly whether cells within that column interact and determine each others' responses.

Lee, Heggelund, Hulme and Creutzfeldt (1977) investigated the distribution of optimal orientations and range of responses of cells in the postlateral gyrus of the striate cortex and found that, while optimal orientation preferences

parallel to the radial bundle were similar, there existed considerable variability. Extraneous sources of variability due to electrode drift and sampling from adjacent columns were excluded by this study. In the monkey, recording from foveal striate cortex, Bauer (Bauer, 1982; Bauer, Dow, Snyder and Vautin, 1983) have reported discontinuity in the orientation column between supra- and infra-granular layers with cells exhibiting marked differences in optimal orientation above and below lamina IV.

Further evidence against the discrete representation of orientation across the cortex is provided by the work of Albus (1975) who investigated the spatial arrangement of orientation in long penetrations crossing laminae in tracks oblique and tangential to the cortical surface, again in the postlateral gyrus of the cat. In contrast to the approach of Hubel and Wiesel of recording only the preferred orientation of successively recorded neurones, Albus compared the preferred orientation and tuning width in pairs of cells separated by 200 microns in tangential penetrations. This revealed that, in both the medio/lateral and antero/posterior directions the difference in preferred orientation between the adjacent cells was small and of the order of 30 degrees or less, with a superimposed variation of 5-10 degrees in a typical sequence. In addition, in some penetrations, the preferred orientation did not change over a considerable distance. In a few cases, differences of more than 40 degrees between successive neurones were seen but abrupt changes were limited to cortical regions where two regularly organized areas partially overlapped each other. Considering the overlap in tuning of

adjacent cells in tangential and vertical penetrations and the scatter in preferred orientation in vertical penetrations it is difficult to reconcile these results with a discrete representation. It is interesting to note that a continuous representation of orientation was apparent in Hubel and Wiesel's study using tangential penetrations in the striate cortex of the monkey (Hubel and Wiesel, 1974) though a discrete representation was considered to exist in the cat (Hubel and Wiesel, 1962). Hubel and Wiesel (1974) were, however, unwilling to accept continuous representation of orientation in monkey striate cortex, arguing that orientation columns were too thin to be resolved in tangential penetrations, that occasional abrupt discontinuities in the representation of orientation in tangential penetrations were seen, and, in perpendicular penetrations, similar preferred orientations were found for successively recorded units.

The de-oxyglucose method for the measurement of local cerebral glucose utilization (Plum, Gjedde and Samson, 1976; Sokoloff, Reivich, Kennedy, Des Rossiers, Patlak, Pettigrew, Sakurada and Shinohara, 1977) has been used as a technique to establish the anatomical basis of the orientation column in a variety of species (Johle and Sokoloff, 1976; Stryker, Hubel and Wiesel, 1977; Lang and Henn, 1980; Hubel, Wiesel and Stryker, 1978; Humphrey, Skeen and Norton, 1980). Carbon 14 labelled de-oxyglucose is incorporated by nerve cells in amounts proportional to their metabolic activity, which in turn is related to their neural activity (Plum, Gjedde and Samson, 1976; Sokoloff, Reivich, Kennedy, Des Rossiers, Patlak, Pettigrew, Sakurada and Shinohara, 1977).

Autoradiographic pictures of de-oxyglucose labelled brain
sections do not show neural structures but regional
differences in grain density which correspond to differences
in glucose uptake between areas of the brain. This method is
employed in the present context to map the cortical sites of
increased metabolic activity produced by visual stimulation
with stripes of a single orientation. These studies produce
results consistent with the columnar hypothesis;
autoradiographs of striate cortex show vertical bands of label
extending through the cortical thickness in the cat (Stryker,
Hubel and Wiesel, 1977; Hubel, Wiesel and Stryker, 1978;
Humphrey, Skeen and Norton, 1980), tree shrew (Skeen,
Humphrey, Norton and Hall, 1978) and, in the monkey,
interrupted in lamina IVc, (Hubel, Wiesel and Stryker, 1978).
Additionally, Humphrey, Skeen and Norton, (1980) reported
that, in the tree shrew, de-oxyglucose labelling confirmed a
pattern of anisotropic distribution of orientation selective
cells across the cortex previously reported by Humphrey and
Norton (1980) from physiological recordings. A test of the
assumed correspondence between stripes revealed by the
de-oxyglucose method and columns revealed by microelectrode
methods was made by Schoppmann and Stryker (1981) in the cat.
A first stage in the experiment established preferred
orientations of neurones at known positions and then the same
animals were stimulated with full-field patterns of stripes of
a single orientation and measurements were made of glucose
uptake at the sites of the cortical units recorded previously.
The centres of densely labelled cortical columns were found to
contain cells selective for the stimulus orientation of the
stripe pattern. Control experiments revealed no columns after

stimulation with a pattern of changing orientation.

Several results from de-oxyglucose mappings of orientation columns are at variance with the columnar concept. Firstly, for the monkey, labelled columns have been reported in conditions in which stimuli of many orientations are presented (Hendrikson and Wilson, 1979; Horton and Hubel, 1980; Humphrey and Hendrikson 1980; and Hendrikson, Hunt and We, 1980). Secondly, at least two studies have reported marked variation in label density from layer to layer outside lamina IV both in width and density of labelling in autoradiographs after stimulation with a single orientation (Hubel, Wiesel and Stryker, 1978; Albus, 1979). Though laminar differences in width of labelling are clearly incompatible with the columnar hypothesis, laminar differences in label density might be accommodated if these differences correlated with laminar differences in cell density. These two variables are, however, not correlated (Hubel, Wiesel and Stryker, 1978). A further difficulty is raised by studies in which an alternative index of metabolic activity is compared with de-oxyglucose labelling. Horton and Hubel (1981) compared staining for cytochrome oxidase (a mitochondrial enzyme) with de-oxyglucose labelling. Stimuli were monocular presentations of black/white stripes at all orientations or a single orientation. In the former case, the rows of patches with de-oxyglucose autoradiography lay in register with the cytochrome oxidase patches but, for the latter condition, de-oxyglucose label formed a lattice that included the cytochrome oxidase patches but was more extensive. The conclusion was that either de-oxyglucose does not label

orientation columns at all, or that orientation columns coalesce in areas marked by cytochrome oxidase stain. An unresolved complication is the reported species difference in cytochrome oxidase patches, being present in primates (Humphrey and Hendrikson, 1980; Horton and Hubel, 1981) but absent in non-primates (Horton and Hubel, 1981).

The rationale of the de-oxyglucose approach is open to question. It may be argued that the type of experiment described represents no more than a refined version of the type of experiment which initiated the columnar concept. What it re-emphasizes is that if one takes some measure of preferred orientation, be it reflected in the response recorded electrophysiologically from successive units or cells labelled by de-oxyglucose, then the cells within a vertical array share the same mean orientation. Whilst de-oxyglucose studies produce results consistent with a columnar hypothesis they equally produce results in accord with continuous representation of orientation; the method does not overcome the recurring problem for the columnar hypothesis, the provision of evidence of a columnar boundary. The determination of columns by differences in the relative density of labelling between adjacent areas in autoradiographs lacks the degree of resolution required for establishing an anatomical boundary. Furthermore, the method can be used to support continuous representation of orientation (Albus, 1979).

One can consider the column from the viewpoint of an array of cells whose response properties are linked in a

chain, the response of each determined by the preceding member. From this perspective it becomes interesting to evaluate the response identity of members of a column. Creutzfeldt, Innocenti and Brooks (1974) made comparisons between pairs of neurones simultaneously recorded with the same electrode. Contrast bars were used as stimuli and the parameters of the moving bar were optimized for the first encountered cell in the penetration. Cells were classified as being small ERF (small excitatory receptive field) or large ERF (large excitatory receptive field), a categorization closely corresponding to the simple/complex dichotomy. The study revealed that excitatory connections are not a common feature of connectivity within a column. Four features of response led to this conclusion: (1) a comparison of ERFs; (2) a comparison of locations within the receptive field; (3) directional selectivity to forward and backward motion of the bar; (4) amplitude of response. In each case no correspondence of response was found.

In the same context, Towe (1975) has pointed out that whereas a topographic model of the cortex allows considerable variation in the size and shape of receptive fields of neurones of the same column, the columnar model requires that they all be nearly identical. Laminar differences in receptive field geometry (Palmer and Rosenquist, 1974; Singer, Tretter and Cynader, 1975; Sherman, Watkins and Wilson, 1976; Wilson and Sherman, 1976; Gilbert, 1977; Henry, Lund and Harvey, 1978; Leventhal and Hirsch, 1978; Gilbert and Wiesel, 1979; Henry, Harvey and Lund, 1979) argue against the columnar principle.

Toyama, Kimura and Tanaka (1981a, b) have approached the problem of intracolumnar interactions using a cross-correlation technique. Three types of inter-neuronal interaction were revealed in this study:-

(1) Joint excitation of two cortical neurones. This was characterized by a positive correlation in response with no delay. Such behaviour was attributed to common excitatory inputs from the lateral geniculate fibres and was typical of half of the neurones studied (105/208).

(2) Delayed excitation, within the monosynaptic range of one cell following the excitation of the other, representing excitatory connections through intracortical routes and typical of approximately one in ten neurones (24/208).

(3) Delayed inhibition of one cell following the excitation of the other, representing inhibitory interactions through intracortical connections and typical of approximately one in ten neurones (26/208).

These patterns of activity had a laminar distribution. Joint excitation was a feature of cells distributed in layers III-IV, i.e. those cells which receive monosynaptic input from the LGN (Toyama, Maekawa and Takada, 1973; Toyama, Matsunami, Ohno and Tokashiki, 1974; Watanabe, Konishi and Creutzfeldt, 1966), and a feature of all cell types except the hypercomplex II category (complex cells with end-inhibition). Delayed excitation was a feaure of cells distributed in the border region between granular and supragranular layers in the case of the source cell, and the upper part of the supragranular layer in the case of the target cell. Such interactions were only found from complex to complex cells and

from complex to hypercomplex type II - i.e. no excitatory
links were found from simple to complex cells. Intracortical
inhibition was confined to four combinations, namely: from
a(on), non-oriented cells with excitatory "on" responses, or
a(off) non-oriented cells with excitatory "off" responses to
simple cells; from simple to complex cells; from a(on) or
a(off) to simple cells; from a(on) or a(off) to complex cells
or between a(on) and a(off) cells. Only one other study, that
of Singer, Tretter and Cynader (1975), has reported the
presence of non-oriented cells in cat striate cortex; their
monosynaptic type 1 cells included some non-oriented cells.
The existence of a class of non-oriented cells is not a
commonly accepted feature of cat striate cortex.

In summary, both studies would suggest that excitatory
connections are not a common feature of interactions among
members of the same column, though Toyama, Kimura and Tanaka's
(1981a, b) study does indicate that where excitatory
connections do take place, they are between members of the
same or adjacent orientation columns. Also, when such links do
occur, they are limited in laminar distribution and are not
between simple and complex cells, in that order. The
demonstration of the second study here, that where such links
do exist this kind of linkage does not take place between
simple and complex cells, is conjectural since on other
grounds it would appear that such links between simple and
complex cells (in that order) may exist. This will be
returned to in the following chapter. It does not undermine
the general point about the lack of excitatory connections.

It has already been argued that the afferent input to the striate cortex is considerably more extensive than would be expected from a columnar organization. The efferent output is likewise extensive, showing a laminar pattern with specific target sites. Lund (1981) has argued that with the possible exception of laminae I, IVa and IVc in the monkey, every lamina of the striate cortex gives rise to efferent projections and that these efferents are segregated from one another, projecting to different destinations and probably conveying different information. Such a pattern, she has argued, is incompatible with a columnar organization for it implies marked differences in organization at different depths, in contradiction to the columnar principle of a common pattern of organization from the pia to the white matter. With most laminae projecting out of the hypothetical column, a pattern of connections emerges which argues against the intracolumnar pattern of connectivity and against a vertical array of cells so linked to provide a functional entity as implied by the column. Indeed, the point is underscored by anatomical (Szentagothai, 1973; Lund and Booth, 1975; Garey, 1976; Lund, 1976) and physiological evidence (Singer, Tretter and Cynader, 1975; Ito, Sanides and Creutzfeldt, 1977) for monosynaptic termination of geniculate fibres on the apical dendrites of lamina V pyramidal neurones, substantial numbers of which project directly out of the cortex to the tectum (Palmer and Rosenquist, 1974; Gilbert and Kelly, 1975). Such patterns of efferent projections as highlighted by Lund are manifest for both the monkey and cat. Area 17 of the cat and monkey show similarities in the organization of the efferent pathways (Palmer and Rosenquist, 1974; Gilbert and Kelly,

1975; Magalhaes-Castro, Saraiva and Magalhaes-Castro, 1975; Martinez, Millan and Hollander, 1975; Lund, 1979, 1981a). In both species lamina VI pyramidal neurones project to the dorsal lateral geniculate nucleus, lamina V projects to the superior colliculus and pulvinar, laminae IIIa and II of the cat project to area 18 and 19, and lamina IIB provides a projection, together with efferent streams from more superficial laminae, to the Clare-Bishop area.

From the preceding discussion it will be apparent that the proposition that the orientation column exists as an anatomical and functional entity has become untenable. This precludes neither excitatory connections of the type supposed by Hubel and Wiesel, nor vertical interactions within the cortex but it denies the axiom that the presentation of a particular orientation of a moving contrast bar uniquely gives rise to activity in an anatomically segregated array of cells defined by a column. On presentation of such a stimulus, cells vertically (Lee, Heggelund, Hulme and Creutzfeldt, 1977) or horizontally (Albus, 1975) close to a hypothetical column respond to varying extents. Such an aggregation of cells forms an "orientation sub-unit" (Albus, 1975, 1979). This "sub-unit" consists of cells which respond at all to a particular orientation. These cells are vertically aligned through all layers and are on average 200 microns (range 25-450 microns) in the horizontal direction to either side from the centre of an iso-orientation band or spot. Sensitivity to the orientation functionally represented by the sub-unit decreases with increasing distance from the centre band or centre spot respectively. It will be apparent from

the concept of an orientation sub-unit, comprising all those cells which respond at all to a particular orientation that, in contrast to the columnar concept, a small change in stimulus results not in a "switching off" of one column and the "switching on" of the next column but a shift in both the degree of response of those cells previously responding and also in the population of cells responding. The concept of the orientation sub-unit implies that each sub-unit has indeterminate boundaries and that it shares cells with its neighbours. The type of spatial and functional organization of the sub-unit implies by itself that the orientation domain has a continuous representation across the cortex.

1.6 The Mechanism of Orientation and Direction Selectivity in Hubel and Wiesel's Model

The responses of striate cortical cells to moving oriented contrast bars can, according to the model, be predicted and explained from a knowledge of the sub-division of the simple cell receptive field. Partitioning of the receptive field should solely reflect the afferent input and its transformation at the geniculo-cortical synapse. Orientation and direction selectivities are determined by interactions within a unitary input to the simple cell.

The specific requirement of the afferent input for the model to be valid is that the type of receptive field organization shown by the simple cell is determined by the convergence and alignment of the geniculate fibres so as to transform the centre-surround organization into that of

elongated fields with division into on and off regions. Colonnier (1964) provided a model of how that convergence might be brought about. The incoming lateral geniculate axons, presumed to retain the topographical arrangement of the retina, would be grouped upon the cortical cells in relation to the latter's dendritic tree. Since for the majority of stellate cells the dendritic fields are elongated in the tangential plane, (Colonnier, 1964; Seldon and Von Keyserlingk, 1978), the orientation of the elongated dendritic tree would permit a preferential selectivity by the recipient cells for groups of oriented axons; the preferential orientation of axons and dendrites in most layers of the cortex results in a focusing of any one group of specifically oriented axons upon similarly oriented dendrites. The functional significance of dendritic geometry remains conjectural (see chapter two). There is some evidence of preferential elongations being determined by factors of gross anatomy rather than functional considerations at the neuronal level (see Seldon and Keyserlingk, 1978 for discussion). However, substantial physiological and anatomical evidence argues against convergence and therefore whatever functional role may be attributed to dendritic morphology it cannot include one of aligning convergent geniculate fibres.

The majority of evidence against convergence is physiological. Creutzfeldt and Ito (1968), from intracellular recordings, reported that each neurone recorded had 2-4 overlapping areas of off or on excitation or inhibition. Each of these areas had the functional properties of a single geniculo-cortical off or on centre fibre with their receptive

field centres separated by 1-3 degrees. Also, from a knowledge of the average firing frequency of afferent fibres and measurements of post-synaptic potentials an estimate of the number of afferents causing those post-synaptic potentials was made of two to four geniculate fibres.

Wilson and Sherman (1976) reported that the receptive field widths for simple cells closely parallel those for geniculate cells at all eccentricities, being consistent with one or a few geniculate neurones providing the excitatory input to the simple cell. Creutzfeldt, Benevento and Kuhnt (1976), from intracellular recordings, revealed the LGN input to cells to be derived from a small retinal area and of a size comparable to the sizes of central excitatory fields found at lower levels of the visual pathway. Lee, Cleland and Creutzfeldt (1977) were able to make simultaneous recordings from retinal and cortical cells and found that the receptive fields were well superimposed and concentric within 0.5 degrees. In conjunction with the finding of the scatter of the receptive field centres of ganglion cells projecting to a single LGN cell being maximally 0.5 degrees (Levick, Cleland and Dubin, 1972), the result was interpreted as evidence that cortical cells received input from individual axons from the LGN. Sillito et al (Berardi, Kemp, Wilson and Sillito, 1980; Sillito, Kemp, Wilson and Berardi, 1980) found that, following the iontophoretic application of bicuculline, the receptive field dimensions of simple cells judged by moving bar stimuli at optimal and orthogonal orientations corresponded with expectations from a single LGNd cell input. Tsumoto, Eckart and Creutzfeldt (1979) have reported the same result.

Bullier, Mustari and Henry (1982), considering the question of brisk-sustained and brisk-transient fibre convergence, reported differences between the two populations with input to simple cells from 1-2 fibres for brisk transient and 2-20 for brisk sustained. For both populations, mean numbers indicated little convergence.

Those studies which have considered the spatial distribution of the afferent input (Creutzfeldt and Ito, 1968; Schiller, Finlay and Volman, 1976b; Lee, Cleland and Creutzfeldt, 1977; Berardi, Kemp, Wilson and Sillito, 1980; Sillito, Kemp, Wilson and Berardi, 1980; Bullier, Mustari and Henry, 1982) indicate that, in the absence of inhibitory mechanisms, the component of the receptive fields of simple cells attributable to the afferent input displays circular symmetry. It would appear that the division of the simple cell receptive field into regions responding to opposite contrasts is dependent on intracortical inhibition since Sillito (1975) has reported that, following iontophoretic application of bicuculline, simple cells respond to flashed stimuli with mixed on-off responses whether these stimuli are confined to previously determined on or off areas or cover the whole receptive field.

If the organization of the simple cell receptive field into sub-regions, as described by Hubel and Wiesel, is not determined by the afferent input the possibility remains that such an organization, re-attributed to intracortical circuitry, confers upon the simple cell its selectivity for orientation and direction. Indeed, the relatively high degree

of predictability of preferred orientation from the layout of
the receptive field is consistent with this.

The relationship between preferred orientation or
orientation selectivity and receptive field geometry has been
investigated in several studies. Creutzfeldt, Kuhnt and
Benevento (1974) found that whilst the excitatory areas of
cortical cells were mostly slightly elongated, this elongation
was not systematically along the axis of optimal orientation.
Plotting the receptive fields of simple cells with flashed
spots, Schiller, Finlay and Volman (1976b) reported these to
be circular or slightly elliptical, although the long axis did
not necessarily fall along the axis of preferred orientation.
Watkins and Berkley (1974), though noting that in general
orientation selectivity is related to receptive field size,
found only a weak correlation between orientation selectivity
and receptive field geometry. Schiller, Finlay and Volman
(1976b) investigated the predictions: (1) that cells with
weak flanks should be more broadly tuned than cells with
strong flanks; (2) the orientation specifity of cells with
bipartite fields should depend on the spatial separation
between the sub-fields and the length of the sub-fields along
the axis of orientation; and (3) that cells with tripartite
fields might be expected to be sharply tuned since they have
two well-defined flanking zones. A comparison of tuning for
various classes of simple cells revealed that the tuning
specificity of cells with only single receptive field zones
was comparable to those in other categories, and cells with
multiple receptive field zones were found to be the most
poorly tuned (though the sample size was small). Comparing

orientation selectivity with measures of receptive field length, centre-to-centre sub-region separation and centre-to-centre separation divided by receptive field length, yielded low correlations (r = -0.25; r = 0.03; r = 0.29).

Orientation selectivity was thought, by Hubel and Wiesel (1962), to be determined by summation of response within a region and antagonism between sub-regions of the receptive field, the antagonism being presumed to reflect inhibitory interactions at the geniculate level. The increased response associated with increased bar length has been confirmed repeatedly (e.g. Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Schiller, Finlay and Volman, 1976b; Hammond and Andrews, 1978a, b, c). That this does not reflect increased recruitment of afferent fibres will be evident from the preceding discussion of the limited geniculate fibre input to individual simple cells (Creutzfeldt and Ito, 1968; Creutzfeldt, Benevento and Kuhnt, 1974; Creutzfeldt, Innocenti and Brooks, 1974; Wilson and Sherman, 1976; Lee, Cleland and Creutzfeldt, 1977; Sillito, Kemp, Wilson and Sillito, 1980) and its spatial distribution (Creutzfeldt and Ito, 1968; Schiller, Finlay and Volman, 1976b; Lee, Cleland and Creutzfeldt, 1977). Sillito, Kemp, Wilson and Berardi (1980) therefore argue that increased response associated with increased stimulus length is not a product of spatial summation but either increasing disinhibition evoked by the change in stimulus length or subliminal facilitatory effects present at all orientations but normally blanked by the inhibition at non-optimal orientations.

Equally, neither antagonism between centre and surround at the geniculate level, nor interactions between sub-regions of the simple cell receptive field, as plotted with stationary bars, can play any role in orientation tuning. At the geniculate level, Dreher and Sanderson (1973) have reported that moving bars simultaneously covering centre and surround produce only excitatory responses. In the second case, for the proposition to be correct, the inhibitory components of the receptive field of the simple cell would have to be coincident with the borders between sub-regions mapped with flashed bars. Spatially distinct inhibitory sub-regions within the receptive field have been reported by Creutzfeldt and Ito (1968), Henry, Bishop and Coombs (1969), Bishop, Coombs and Henry (1971 a, b), Bishop and Henry (1972) and Bishop, Coombs and Henry (1973), amongst others. When these sub-regions are located using the monocular or binocular conditioning method of Henry, Bishop and Coombs (1969), they are frequently not in register with the regions mapped with stationary or moving stimuli (Henry, Bishop and Coombs, 1969; Bishop, Coombs and Henry, 1971 a, b; Bishop, Coombs and Henry, 1973; Schiller, Finlay and Volman, 1976e). The schematic model of the simple cell incorporating such side-band inhibition is taken up in the context of models invoking intracortical inhibition.

Directional selectivity was viewed also to be the product of the disposition of the receptive field regions, as a product of synergistic action between them. Several predictions follow from the model.

(1) Stimulus movements confined to either discharge region

would not show directional selectivity.

(2) Directional selectivity would not be shown for a moving edge crossing the receptive field.

(3) A directional preference with one sign of contrast would be reversed with contrast reversal.

None of these predictions has been fulfilled. It has been demonstrated that regions smaller than "on" or "off" areas show directional selectivity (Bishop, Dreher and Henry, 1972; Bishop, Goodwin and Henry, 1973; Goodwin, Henry and Bishop, 1975) and that the preferred direction of motion of a contrast bar is not invariably predictable from the spatial layout of the receptive field (Bishop, Dreher and Henry, 1972; Henry and Bishop, 1972; Henry, Dreher and Bishop, 1974; Goodwin, Henry and Bishop, 1975; Nothdurft, 1976; Schiller, Finlay and Volman, 1976a; and Henry, 1977). Directional selectivity has been demonstrated for edges (e.g. Schiller, Finlay and Volman, 1976a). Furthermore, some simple cells show a directional preference independent of contrast reversal (Bishop, Coombs and Henry, 1971a; Emerson and Gerstein, 1977; Albus, 1980). However, the disposition of the regions probably has some bearing on the strength of discharge to moving bars of different widths and contrast polarity (Bishop, Coombs and Henry, 1971b).

A specific addition to the original model was the suggestion of the reinforcement of the "surround zones" by fibres of the opposite type (for a simple cell whose main input is on-centre, the antagonistic region would be reinforced by off-centre fibres, and vice versa). A number of lines of evidence argue against convergence of on- and

off-centre neurones onto individual simple cells. The studies
of Dreher and Sanderson (1973) and Bishop, Goodwin and Henry
(1973) together indicate that the responses of simple cells to
moving contrast bars are consistent with individual simple
cells receiving either on- or off-fibre input, but not both.
In terms of phase behaviour, simple cells have been reported
as falling into two groups (Lee, Elepfandt and Virsu, 1981b)
corresponding to on- and off-centre cells at lower levels in
the visual pathway (Lee, Elepfandt and Virsu, 1981a).
Bullier, Mustari and Henry (1982) established the signature
for LGN neurones with moving and stationary bars and
identified the signature in the responses of simple cells
which indicated that the majority were explicable in terms of
a non-mixed input.

However, Lee, Elepfandt and Virsu (1981b) and Bullier,
Mustari and Henry (1982) have reported a minority of neurones
whose phase or signature behaviour is indicative of a mixed
input. It remains conjectural whether those neurones
represent higher order simple cells with "mixing" occurring
intracortically or cells receiving mixed input at the
geniculo-cortical synapse. However, where such mixing occurs
it would appear to have no role in determining directional
selectivity. Schiller (1982) made use of Slaughter and
Miller's (1981) demonstration that in the isolated eye cup of
the mudpuppy and rabbit, DL-2-amino-4-phosphonobutyric acid
(APB) reversibly blocks the "on" responses in the retina. The
directional selectivity of cortical simple cells was measured
before, during and after blocking the retinal "on" system.
The directional preferences of the units was unaltered by APB

infusion thus showing directional selectivity not to be
dependent on interactions between "on" and "off" channels.

In summary, whilst the subdivision of the simple cell
receptive field plotted with flashed bars provides some
indication of the preferred orientation for a moving bar, that
division neither reflects the distribution of the afferent
input nor the mechanism generating that selectivity. Neither
can one explain the directional selectivity shown by the
simple cell with reference to that scheme.

1.7. Implications.

The primary role of the afferent input in determining the
orientation and direction selectivity of cortical neurones is
not supported. Since each individual cortical neurone
receives, at the most, input from a few geniculate fibres the
geometry of the afferent input puts few constraints on the
form of the receptive field. The functional properties
attributable to the afferent input from the lateral geniculate
nucleus are limited to the contributions of individual fibres,
from their centre-surround organization and the functional
properties of different fibre types. Consideration is given
in subsequent discussion to whether some of the functional
differences between simple and complex cells are a product of
different geniculate fibre inputs. The widespread laminar
distribution of afferent fibres means that all cells within a
hypothetical column are potential recipients of direct
mono-synaptic input. Contact between afferent input and
individual cortical neurones is constrained neither by

morphological nor receptive field classes and so no neurone type can occupy a pivotal position in the progression of intracortical circuitry from the afferent input.

The implications of the columnar model with a discrete representation of orientation, that the functional role of striate neurones is defined by their optimal orientation preference and that cells in close vertical proximity with identical optimal orientation preference comprise a functional unit, runs counter to physiological and anatomical evidence. Since striate neurones do not show orientation selectivity but respond with a gradation of response to a range of orientations, their functional properties may only be described by their tuning characteristics. The constraints placed on intracortical organization by the discrete representation of orientation have been contrasted by Towe (1975) with the functional implications of continuous representation of orientation assumed in a topographical model of the cortex.

"The former (a topographic model) views the cerebral cortex as a continuous tissue wherein each indiviual neurone functions as a fundamental unit, being free to discharge in relation to various subsets of its neighbours. The latter parcels the cerebral cortex into discrete sets of neurones, termed columns, such that each column acts as an elementary functional unit - each neurone within a column can discharge with one and only one set of neurones - those comprising its own column."

As Lund (1976) has pointed out, since the most obvious progression of synaptic relays in area 17 seems to be between laminae, these kinds of connections would underlie the physiological impression of vertically organized columns or slabs - or that the whole set of links would create a unit of function and that all the outputs from such a unit might constitute a set of information common to the unit. There would, however, appear to be neither anatomical evidence for a segregation of columns nor physiological support for the column constituting a functional entity. As suggested by MacKay (1976), there seem to be very few cases in which columnar organization means abrupt functional discontinuity between cells of a given layer. In most cases it means only that cells immediately below one another in a radial penetration have similarly related fields and frequently, but not always, similar stimulus preferences. The column may be fractionated with different patterns of organization linked to lamination. Every lamina of the striate cortex, with the exceptions of laminae I and IV, contains cells projecting extrinsically and it would seem likely, with those outputs projecting to different areas with different functional roles, that each projection out of area 17 carries a particular kind of information or weighting in terms of specific function. Furthermore, each lamina not only projects to different destinations but has a different relationship to the distribution of thalamic afferents and to the patterns of connections intrinsic to the striate cortex. These diverse patterns of connectivity cannot be acounted for by a simple serial chain.

The context set for subsequent discussion is one in which the orientation/direction selectivity of cortical neurones is seen to be a product of intracortical circuitry. Alternative models are presented and evaluated against current knowledge of the pattern of intracortical connections derived from anatomical and physiological studies. Emergent from the discussion is the dependence of orientation/direction selectivity on intracortical inhibition and the need to posit separate mechanisms to explain the orientation and direction selective properties of cortical neurones. The contributions of these separate mechanisms are assessed by determining the tuning curves for stimuli in which the parameters of orientation and direction are dissociated.

CHAPTER TWO: THE ROLE OF INTRACORTICAL CIRCUITRY IN THE
MEDIATION OF ORIENTATION AND DIRECTION SELECTIVE MECHANISMS

2.1 Models for the Role of Intracortical Inhibition
2.1a The Models of the Canberra Group

Bishop and associates (Bishop, Coombs and Henry, 1971b)
proposed a model of the simple cell which potentially overcame
two shortcomings in Hubel and Wiesel's model: the poor
predictive value of a receptive field structure plotted with
stationary bars for moving stimuli (Bishop, Coombs and Henry,
1971a; Henry and Bishop, 1972); and the absence of
inhibitory interactions between centre and surround at the
geniculate level (Dreher and Sanderson, 1973). Receptive
field structure was elaborated with moving bars and inhibitory
interactions re-attributed to the cortical level. In the
absence of a resting discharge for the majority of simple
cells, inhibition was measured against a response induced by a
conditioning stimulus (Bishop, Coombs and Henry, 1971b). The
"dynamic" receptive field was plotted as a peri-stimulus time
histogram (PSTH) to a moving bar at the cell's preferred
orientation and moving in its preferred direction. In
skeleton form, the receptive field determined in this way
comprises a central discharge zone flanked by inhibitory
side-bands with non-responding end-zones (fig. 2.1).

In this model, the central discharge zone is formed from
aligned receptive fields of converging fibres from the lateral
geniculate nucleus and the sidebands arise from inhibitory
intracortical circuitry. A reconciliation with Hubel and

The Model of Bishop and Associates.

The figure illustrates receptive field structure determined
in the PSTH to a moving bar in preferred and non-preferred
directions for the cell. In the preferred direction,
receptive field structure has three components; a central
discharge zone (black) formed by converging afferent fibres,
inhibitory side-bands flanking the excitatory region and
non-responding end-zones. In the non-preferred direction,
the non-responding end-zones become part of the inhibitory
component of the receptive field.

Filled circles; complete inhibition.
Open circles: partial inhibition.

(after Henry and Bishop, 1972).

NON-RESPONDING
END-ZONE

INHIBITORY SIDEBANDS

PREFERRED DIRECTION

1°

NON-PREFERRED DIRECTION
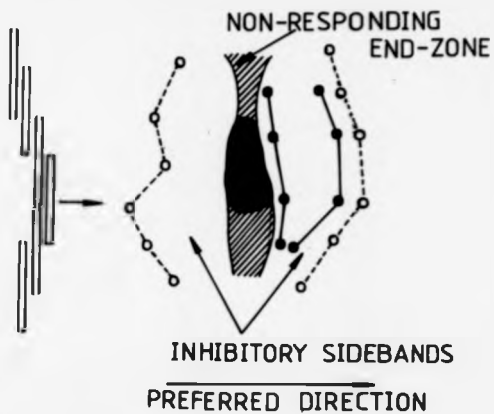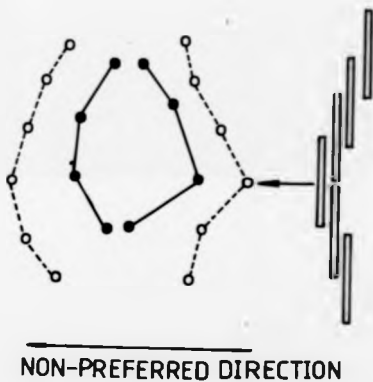
Wiesel's model (1962, 1963) was suggested by attributing the
structure of the "static" receptive field, plotted with
stationary bars, to the excitatory input and the "dynamic"
structure to intracortical circuitry. In addition to the
assumption contained in Hubel and Wiesel's model of
convergence of afferent fibres, a further assumption was
introduced; that of a fixed spatial relationship between
intracortical inhibition and afferent excitation. This
assumption also applied to the model for direction selectivity
later developed by Goodwin, Henry and Bishop, (1975) and
Goodwin and Henry (1975).

Several variants of the model were elaborated, the
end-product of which was a spatial and functional sub-division
of the simple cell receptive field (Henry, Dreher and Bishop,
1974; Henry, Bishop and Dreher, 1974; · Goodwin and Henry,
1975). In an early version (Bishop, Coombs and Henry, 1971b),
both the orientation and direction selective properties of
simple cells were attributed to the sidebands. Orientation
selectivity was seen as a product of summation of response
within the central discharge zone and inhibition mediated by
the sidebands.

Since for long bars direction is necessarily orthogonal
to orientation (Henry, Dreher and Bishop, 1974), direction
selectivity was seen as a parameter limiting response to one
of two possible directions set by the cell's preferred
orientation. Bishop, Coombs and Henry (1971b) proposed that
direction selectivity is a product of events preceding the
entry of the stimulus into the central discharge zone.

Direction selectivity would be a consequence of disinhibition to a stimulus starting to move in the preferred direction followed by summation of response in the central discharge zone. In the non-preferred direction, response would be limited or prevented by the non-release of tonic inhibition and by inhibition spreading ahead of stimulus movement. Inhibition of response was considered more localised in action than in the model put forward by Barlow and Levick (1965) to account for the direction selectivity in the rabbit's retina. Inhibition was assumed to be limited to action of those geniculate cells immediately preceding the central discharge zone. Feedforward inhibition was transferred to the discharge centre in Goodwin, Henry and Bishop's (1975) model.

The demonstration of a direction selective response for a stimulus wholly contained within the central discharge zone (Bishop, Goodwin and Henry, 1973) clearly indicated that the directional properties of simple cells are not dependent on side-band inhibition (Bishop, Goodwin and Henry, 1973). The side-bands were retained in the model as a mechanism for generating orientation selectivity. The side-bands were functionally linked with a direction-selective mechanism (Goodwin, Henry and Bishop, 1975) as a barrier to the spread of inhibition generated within the central discharge zone. Orientation selectivity would be generated by convergent afferent fibres conferring on the simple cell a rudimentary orientation bias which would be sharpened by sideband inhibition.

2.1b Direction Selectivity Produced by Feedforward Inhibition: The Model of Goodwin, Henry and Bishop

The overall goal of the model was to account for the organization of the discharge zone which prevents response in the non-preferred direction. Barlow and Levick (1965) had earlier shown the direction selectivity of rabbit retinal ganglion cells to be dependent on inhibitory interactions between directionally unselective sub-units within the receptive field. In testing the validity of the model, Goodwin, Henry and Bishop (1975) argued that while the simple cell is not divided into sub-units, direction selectivity can be seen as a product of feedforward inhibition. Evidence against sub-units was that the threshold displacement of a contrast bar is direction selective (Goodwin, Henry and Bishop, 1975). Quantitative analysis of responses in preferred and non-preferred directions implicated suppression of response in the non-preferred direction as the basis of direction selectivity. The major part of the study was therefore addressed to evaluation of the conditions under which direction-specific inhibition is generated.

It was suggested (Goodwin, Henry and Bishop, 1975) that the spread of inhibition mediating direction selectivity depends on two parameters: (1) the spread of inhibition curve - describing the spread of inhibition ahead of a moving stimulus, taking the same form at different locations within the receptive field and decaying in intensity as a function of distance from a moving edge; and (2) location within the receptive field - as reflected in the sensitivity profile to a

stationary flashed bar determined by the profiles of the excitatory and inhibitory inputs across the discharge zone. Goodwin, Henry and Bishop (1975) found inhibition to be distributed over the whole of the discharge area but were unable to assess the contributions of these two parameters. It was however suggested that, at any location, direction-selective inhibition is maintained as long as the edge remains in position.

The model developed by Goodwin, Henry and Bishop (1975) has components from geniculate and cortical levels. Cortical inhibition has a role of limiting the directional bias present at the geniculate level to produce a direction selective response. At retinal and geniculate levels, on- and off-centre neurones have a centrifugal or centripetal direction bias (Rodieck and Stone, 1965; Dreher and Sanderson, 1973). As in Bishop, Goodwin and Henry (1973), excitatory input is provided by convergent afferent fibres of either on- or off-centre. Direction selectivity is conferred by blanking out half the receptive field by intracortical inhibition; the direction for which a cell is selective depends on which half of the field is blanked out. Afferent drive to the cortical neurones providing the inhibitory circuitry is suggested to come from mixed on- and off-centre sustained neurones. Input from sustained neurones would ensure that inhibition applied to the simple cell is maintained as long as the edge remains in the field.

Complex cells, in Goodwin and Henry's (1975) scheme, are the recipients of a directionally-tuned input from simple

cells. A similar proposal for complex cells' orientation
selectivity was made by Henry, Dreher and Bishop (1974). Both
models were elaborated for complex cells of the supragranular
layers. Similarities in the directional properties of complex
cells with simple cells in the dimension of the smallest
displacement giving a direction-selective response and in the
role of inhibition in suppressing the response in the
non-preferred direction were reported by Goodwin and Henry
(1975). The essential difference between simple and complex
cells' direction selectivity reported by Goodwin and Henry
(1975) was that, whereas for the simple cell inhibition
suppresses both driven and spontaneous activity, inhibition
suppresses only the driven activity of the complex cell.
Earlier, Barlow and Levick (1965) reported that, for on-off
direction-selective ganglion cells in rabbit, the suppression
of spontaneous activity occurs at the cell where inhibition is
active in initiating direction selectivity. If inhibition
responsible for the generation of direction selectivity fails
to influence the spontaneous activity, complex cells must
receive a directionally tuned excitatory input; driven and
spontaneous activity are derived from different sources
Goodwin and Henry (1975) argued. Complex cells, in Goodwin
and Henry's (1975) scheme are the recipients of a
directionally tuned input from simple cells. Accepting a
parallel model of connectivity between geniculate X and simple
cells and geniculate Y cells and complex cells, those complex
cells receiving Y input were left unaccounted for in the
model.

In a later study, Bishop, Kato and Orban (1980) reported

direction-selective complex cells in cat striate cortex for which suppression of the resting discharge for motion in the non-preferred direction was seen. Such neurones (twelve in total) were located both above and below lamina IV, though two of the four direction-selective cells in laminae II/III had no spontaneous activity and for these, inhibition in the non-preferred direction was only demonstrated against a background discharge to a conditioning stimulus.

It is in establishing the role of feedforward inhibition at the cortical level that the studies of Bishop and associates have made their contribution to the understanding of the stimulus selectivity shown by cortical neurones. The shortcomings of the model of the simple cell developed by Bishop and associates are threefold; in the functional interpretation of inhibition extending outside the central discharge zone, the lack of conceptual development of the relationship between sideband and direction-selective inhibition and leaving unanswered the contribution of stimulus movement to the production of direction-selective inhibition.

2.1c The Mediation of Orientation and Direction Selectivities by Separate Mechanisms: The Model of Schiller, Finlay and Volman

There is a close affinity between the model of the simple cell constructed by Bishop and associates and that put forward by Schiller, Finlay and Volman (1976b, e). The component of the receptive field attributed to intracortical circuitry is virtually identical (fig. 2.2). A primary difference arises

from the observation of Schiller, Finlay and Volman (1976b)
that the excitatory component of the receptive field exhibits
circular symmetry. This precludes a role for the afferent
input in determining the cell's preferred orientation.
Schiller, Finlay and Volman (1976e) gave this role to the
geometry of pyramidal cell dendrites, simple cells being
represented morphologically by pyramidal cells in the model.
Further, on the basis of comparison of the tuning properties
of cortical neurones, Schiller, Finlay and Volman (1976e)
proposed that orientation and direction selectivities are
mediated by separate mechanisms arising from two levels of
inhibition.

The simple/pyramidal cell would have its orientation
properties mediated by inhibitory circuitry associated with
the apical dendrites and its directional properties mediated
by inhibitory circuitry associated with the basal dendrites.
An immediate attraction of the model was that potentially it
could account for the diversity of direction selective
properties shown by simple cells, by assuming an unvarying
pattern of connectivity for the apical dendrites within the
simple cell group, but different basal dendrite patterns. The
arguments advanced by Schiller, Finlay and Volman (1976b)
provide only partial support for the mediation of orientation
and direction selectivities by separate mechanisms. Strong
support for the mediation of direction and orientation tuning
by separate mechanisms is given by the studies of the tuning
of complex cells for bar and texture stimuli (Hammond and
Mackay, 1977; Hammond, 1978, 1979; Hammond and Reck, 1980a,
b). These studies indicate a functional interdependence of

The Model of Schiller, Finlay and Volman.

Orientation and direction selectivities are mediated by separate
mechanisms associated with two levels of inhibition.

(A). Orientation selectivity is derived from inhibitory
circuitry associated with the apical dendrite. The effective
dendritic arborization is bilobed. The axis of orientation is
along the perspective line, where inhibition is ineffective.
The upper layer of interneurones may receive afferent input
directly from the LGN (A), by LGN cells coupled with
reciprocal inhibition (B) or by other pyramidal cells (C).
The lower level of inhibitory interneurones mediate direction
selectivity. Spread of basal dendrites in one direction
provides the basis of selectivity for one direction.

(B) Receptive field structure resulting from the spatial
organization of dendrites illustrated in fig. A. Excitatory
input forms a circular component of the receptive field.
Inhibition mediating orientation selectivity is represented
as two bands either side of the excitatory centre. Inhibition
mediating direction selectivity is distributed to one side
of the excitatory centre.

(after Schiller, Finlay and Volman, 1976b, e).

(A)

(B)

PREFERRED ORIENTATION

EXCITATORY CENTRE

BASAL DENDRITIC FIELD

APICAL DENDRITIC FIELD
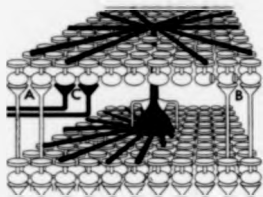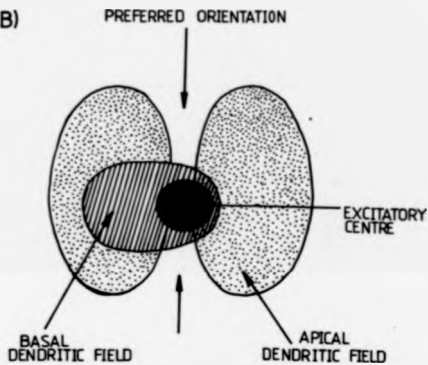
orientation and direction mechanisms. The circuitry mediating these mechanisms, at the single cell level, remains conjectural.

2.1d The Model of Creutzfeldt and Associates

Both Bishop's and Schiller's models assumed that the key to understanding the origin of orientation and direction selectivities lies in the spatial distribution of inhibition within the simple cell receptive field. Each model assumed a hierarchical pattern of intracortical connectivity. A quite different view was taken in the model of Creutzfeldt (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974). A strictly parallel model of connectivity was assumed (Hoffmann and Stone, 1971; Stone and Dreher, 1973; Dreher, Hale and Leventhal, 1978). Intracortical connections were proposed to be restricted to inhibitory pathways from complex to simple cells. Excitatory connections were limited to a role in modulating inhibition. Both simple and complex cells, it was suggested, lie in the same inhibitory network with differences in receptive field structure being quantitative not qualitative. An understanding of the functional properties would therefore rest on an understanding of the properties of the neuronal network. Creutzfeldt, Kuhnt and Benevento (1974) further argued that inhibitory circuitry determining cortical cells' trigger features extends beyond the classical orientation column and that the functional properties of cortical neurones is a product of cross-talk between columns (Benevento, Creutzfeldt and Kuhnt, 1972). That pattern of connectivity

would need to be anisotropic in order to generate the cortical cells' anisotropic trigger features (Creutzfeldt, Kuhnt and Benevento, 1974).

The model embodies the following:

(1) The retino-cortical projection preserves a retino-topic gradient, but is essentially random if only small cortical projection points are considered (Hubel and Wiesel, 1963; Creutzfeldt, Kuhnt and Benevento, 1974; Albus, 1975).

(2) Individual cells are mainly excited by a very restricted number of geniculate fibres, often by only one fibre.

(3) Inhibition of cortical neurones extends over distances which are of the same order, or slightly larger than, the diameters of functional orientation columns.

(4) Though an anisotropy is already apparent in the anisotropy of afferent connections (Albus, 1975), the anisotropy on which the tuning properties of cortical neurones depends is more dependent on the pattern of intracortical connections. The possibility was raised by Benevento, Creutzfeldt and Kuhnt, (1972) that such a pattern of connectivity might be arranged in stripes (or bands) as had been described for the basket cells in the motor cortex by Marin-Padilla (1970).

The major contribution of Creutzfeldt's model has been in illuminating the role of the horizontal organization of the striate cortex. The central point of conjecture of the model has been the extent of horizontal inhibitory interactions and the relative contribution of inhibitory input from columns close to or far from the recipient cells (Hess, Negishi and Creutzfeldt, 1975, Hess, Ostendorf, Sanides, Negishi and

Creutzfeldt, 1976; Sillito, 1976, 1979).

2.2 The Dependence of Orientation and Direction Selectivities on Intracortical Inhibition

The geniculo-cortical synapse may be characterized by anatomical and physiological criteria as excitatory. The synapses formed between afferent fibres and both pyramidal and stellate neurones have asymmetrical thickenings (Colonnier and Rossignol, 1969; Garey and Powell, 1971) associated with excitation (Uchizono, 1965). Stimulation of the afferent pathway by an electrical stimulus (Creutzfeldt, Baumgartner and Schoen, 1956; Jung, Creutzfeldt and Baumgartner, 1957; Li, Ortiz-Galvin, Chou and Howard, 1960; Watanabe, Konishi and Creutzfeldt, 1966), diffuse light (Creutzfeldt, Rosina, Ito and Prost, 1969) or a punctiform light stimulus (Creutzfeldt and Ito, 1968) leads to inhibitory postsynaptic potentials (ipsps) as well as excitatory postsynaptic potentials (epsps). The latency of ipsps, compared with epsps, is regularly delayed by 0.8 msecs. regardless of whether the site of stimulation is the optic chiasm, lateral geniculate nucleus or optic radiation; the delay is therefore intracortical.

The dependence of orientation/direction selectivities of simple and complex cells on intracortical inhibition has been established from intracellular recordings and by pharmacological studies. Benevento, Creutzfeldt and Kuhnt (1972) reported quantitative changes in inhibition, in intracellular recordings from simple and complex cells, when

the orientation and direction of movement of a contrast bar stimulus was changed. This implies that the inhibition of these cells, as well as the suprathreshold excitatory response, is orientation and direction specific. Other intracellular studies have confirmed the result (Creutzfeldt, Kuhnt and Benevento, 1974; Innocenti and Fiore, 1974).

Pharmacological studies have also revealed the dependence of the tuning of both simple and complex cells for orientation and direction on intracortical inhibition (Sillito, 1974b, 1975b, 1976, 1977, 1979; Tsumoto, Eckart and Creutzfeldt, 1979; Ostendorf and Hess, 1975). Additionally, these studies have indicated a differential dependence between simple and complex cells and within the complex cell group (Sillito 1974b, 1975b, 1976, 1979, 1980; Ostendorf and Hess, 1975; Hess, Ostendorf, Sanides, Negishi and Creutzfeldt, 1976; Tsumoto, Eckart and Creutzfeldt, 1979). The putative inhibitory transmitter in the striate cortex, Gamma Amino Butyric Acid (GABA) (Mitchell and Srinivasan, 1969; Iversen, Mitchell and Srinivasan, 1971), is antagonized by the alkaloid bicuculline (Curtis, Duggan, Felix and Johnston, 1970, 1971; Curtis and Johnston, 1974). Bicuculline blocks the inhibition produced by the iontophoretic application of GABA and visually evoked inhibition (Sillito, 1975a). The intravenous, topical and iontophoretic application has been used to assess the relative contributions of intracortical inhibition and tuned excitatory input to the functional properties of simple and complex cells.

Two studies using intravenous administration of

bicuculline produced contradictory results. Daniels and Pettigrew (1973) reported minimal changes in receptive field structure and tuning properties of simple cells but most complex cells showed a loss of orientation selectivity. Using similar techniques, Rose and Blakemore (1974) found negative results for both simple and complex cells. With topical application of bicuculline to the cortex, these authors found broadening of simple cells' orientation tuning but variable results for complex cells.

Little reliance can be placed on the two studies. Sillito (1975b) has pointed out that intravenously injected bicuculline produces changes in excitability of many parts of the nervous system including possible actions on the retina and lateral geniculate body (Straschill and Perwein, 1969; Curtis and Tebecis, 1972). Topical application may produce changes in the overall excitability and hence possible modifications of receptive field properties. These problems are not associated with the iontophoretic application of bicuculline.

Sillito (1974b), in addition to reporting changes in the partitioning of the simple cell receptive field, found cells' orientation and direction selectivities to moving contrast bars reduced following bicuculline application. Often, but not always, this was accompanied by a large increase in magnitude of the evoked response. Confirming the reduction of orientation selectivity, Sillito (1975b) saw elimination of direction selectivity for a few cells after bicuculline application. Tsumoto, Eckart and Creutzfeldt (1979) reported

that while, for a majority of simple cells, direction selectivity was abolished or reduced, orientation selectivity was abolished in no case and reduced in only two of eight cells. For complex cells, these authors found direction selectivity to be abolished or reduced in half the sample of six cells. The resistance of orientation tuning of both simple and complex cells has been reported in the studies of Ostendorf and Hess (1975) and Hess, Negishi and Creutzfeldt, (1975). The possibility of an orientationally tuned input to simple cells or incomplete synaptic blockade by bicuculline was therefore raised.

A resolution of the question came from the work of Tsumoto, Eckart and Creutzfeldt, (1979) and Sillito, Kemp, Wilson and Berardi (1980). Tsumoto, Eckart and Creutzfeldt (1979) used the inhibitor of GABA synthesis 3-mercaptoproprionic acid (MP) (Lamar, 1970; Rodriguez, Alberici and De Robertis, 1972; Rodriguez, Alberici, Robiolo and Mistrorigo, 1973; Karlsson, Fonum, Malthe-Sorenssen and Storm-Mathisen, 1974; Wu, 1975) in combination with bicuculline or given alone. Bicuculline application alone was never found to produce complete elimination of orientation selectivity but combined administration of MP (intravenously) with iontophoretic bicuculline abolished orientation tuning in one third of simple cells. For two out of six complex cells tested, orientation selectivity was abolished under combined application; the sample size was too small to suggest a differential effect of MP on simple and complex cells. In a re-evaluation of simple cell orientation selectivity, Sillito, Kemp, Wilson and Berardi (1980) found that, following

iontophoretic application of the GABA antagonist N-methyl bicuculline, previously sharply tuned simple cells responded equally well to all orientations/directions. The result supported the conclusion that the orientation bias remaining after bicuculline application in previous studies was a consequence of inadequate blockade of synapses.

A differential dependence of the orientation and direction selective properties within the complex cell group has been indicated by the extensive studies of Sillito (1975b, 1976a, b, 1977, 1979). Sillito (1975b) found that the orientation selectivity of complex cells, following the iontophoretic application of bicuculline, was reduced. In many cases, cells subsequently responded to an orientation orthogonal to the optimal with equal magnitude of response. The same study indicated that the direction selectivity of complex cells was less affected than that of simple cells. In addition, when large changes in orientation tuning were seen, the direction selectivity was relatively unaltered. Sillito (1976) found that, for those cells most closely resembling simple cells, bicuculline eliminated or reduced these cells' direction selectivity. However, for all other complex cells, bicuculline had much less effect on direction selectivity, particularly in the case of lamina V complex cells identified with the cortico-tectal neurones in Palmer and Rosenquist's study (1974). For such neurones, a transmitter other than GABA mediating direction selectivity was suggested.

The differences in origin of complex cells' direction selectivity was highlighted in a further study. Sillito

(1977) grouped complex cells into three categories in terms of the origin of their direction selectivity. Type 1 complex cells' direction selectivity was eliminated during bicuculline application. These cells were located in the supragranular layers. The direction selectivity of type 2 complex cells was unaffected by bicuculline despite increases in response magnitude, a block of the action of iontophoretically applied GABA and, in some cases, changes in receptive field properties. Type 2 cells were located both superficial and deep to lamina IV with the majority in lamina V. The type 3 complex cell, whose receptive field properties were seen to be similar to cortico-tectal neurones, showed no elimination of direction selectivity on application of bicuculline, but exhibited a powerful suppression of the resting discharge in response to stimulus motion in the non-preferred direction. For those lamina V neurones, iontophoretic application of ammonium ions revealed a small excitatory response in place of suppression.

These results may be summarized by saying that type 1 cells receive a directionally non-specific excitatory input and that, as for simple cells, the direction selectivity derives from the action of GABA-mediated post-synaptic inhibitory input. Type 2 receive a direction specific excitatory input. For type 3 neurones, the direction selectivity could be dependent, at least in part, on inhibitory processes which are not GABA-mediated.

Within the "standard" complex cell group (Gilbert, 1977) a differential dependence of orientation tuning on

intracortical inhibition has been revealed (Sillito, 1979).
For one group, the orientation tuning was eliminated during
bicuculline application, indicating the excitatory input to
these cells to be non-orientation specific. The other group
of "standard" complex cells, although showing a decrease in
orientation tuning, retained a preference for a range of
orientations that was generally centred around the optimal
orientation. For these cells, it was suggested that the
inhibitory input enhances the orientation tuning of an
excitatory input that is already broadly orientation tuned.
The laminar distribution of the two groups was left unanswered
as was the origin of the orientation selectivity of "special"
complex cells.

2.3 The Representation of Inhibition in the Simple Cell
Receptive Field

Inhibitory side-bands were viewed as a feature of the
receptive field present in simple but absent in complex cells
(Henry, Bishop and Coombs, 1969; Bishop, Coombs and Henry,
1971b; Bishop and Henry, 1972; Henry, Dreher and Bishop,
1974). Though the possibility of side-band inhibition in
complex cells was raised by Goodwin and Henry (1975), Glezer,
Ivanov and Tsherbach, (1973) and Heggelund and Moors (1978),
the majority of studies have reported their absence in the
complex cell receptive field (Wilson and Sherman, 1976;
Schiller, Finlay and Volman, 1976b; Sherman, Watkins and
Wilson, 1976; Leventhal and Hirsch, 1978). Albus and Fries
(1980), in an analysis of data from Fries and Albus (1976) and
Fries, Albus and Creutzfeldt (1977), confirmed the presence of

sidebands in simple cells but also observed them in a minority of complex cells (3 out of 18) when tested with the monocular conditioning technique. These sidebands were non-orientation specific.

Asymmetries in the spatial arrangement of the inhibitory flanks of the simple cell have been reported by Bishop, Goodwin and Henry (1973), Creutzfeldt, Innocenti and Brooks (1974) and Innocenti and Fiore (1974). This suggests that the response to a moving stimulus reflects temporal factors as well as a fixed, spatial receptive field pattern (c.f. Rodieck and Stone, 1965; Bishop, Coombs and Henry, 1971a). Fries and Albus (1976) reported that the majority of simple cells show an asymmetrical zone for one direction of stimulus movement and a symmetrical one for the opposite direction. The dependence of activity profiles on temporal factors and on the contrast of the stimulus was evaluated by these authors. Comparisons were made of response to stationary and moving bars for cells with asymmetrical flanks. Receptive field structure determined with stationary bars was compared with the response to moving bars in the peri-stimulus time histogram (PSTH) and in the activity profile (Bishop, Coombs and Henry, 1971b). The receptive field structure seen in activity profiles was only loosely related to stationary maps of the receptive field. In illustration, for a cell showing an off-centre flanked by two on regions, the activity profile indicated that the inhibitory peaks preceding the discharge coincided with the off region. In the PSTH to a moving bar, the bar was seen to elicit, in the same region, an excitatory response. For this unit, light bar discharges were found to

occur after the dark discharge for both directions of movement
i.e. discharge peaks to light stimuli seem to occur in
different retinal locations according to the direction of
movement. Moving the stimulus over an on zone lying before
the off zone produced only a subliminal response. Thus, the
retinal locus where excitation is evoked depends on the
contrast and on the direction of movement of the stimulus. A
further mismatch between receptive field structure determined
with the PSTH and a stationary bar RF plot was noted for the
optimal movement direction; in the activity profile a further
inhibitory region followed the discharge peak. Fries and
Albus commented that similar inhibitory zones, revealed only
with moving stimuli, can be seen in the PSTHs of responses of
retinal ganglion cells (Rodieck and Stone, 1965) and of LGN
neurones (Dreher and Sanderson, 1973). Fries and Albus also
found in their study that, while "off" zones always
corresponded to inhibitory troughs in the activity profile,
extra inhibitory responses were seen in the profile which were
not related to an area excitable by stationary bars. This
inhibition appears to arise from temporal factors, i.e.
effects associated with stimulus movement.

The weak association between afferent excitation and
inhibitory zones in the receptive field is further
demonstrated in intracellular recordings. Benevento,
Creutzfeldt and Kuhnt (1972) and Creutzfeldt, Kuhnt and
Benevento (1974) both reported little correlation between the
spatial distribution of intracortical inhibition and afferent
excitation. Intracellular recordings have also been used to
assess the relationship between inhibition measured by the

conditioning technique and intracortical inhibition. Innocenti and Fiore (1974) raised the question of whether the suppression of response revealed on an artificially enhanced background activity is due to post-synaptic inhibition or reflects a disfacilitation induced by intrathalamic mechanisms. In support of the latter possibility are the observations of similar patterns of excitation-inhibition seen in the response of geniculate neurones to moving stimuli (Dreher and Sanderson, 1973; Singer and Creutzfeldt, 1970). Innocenti and Fiore (1974) compared responses obtained with the conditioning technique with those seen in intracellular recordings. Extracellularly recorded responses to moving bars at the cell's preferred orientation were classified into four groups according to the sequential order in which excitatory and inhibitory components appeared in the PSTH:

(A) Excitation followed by inhibition (B) Excitatory responses preceded by inhibitory responses (C) Symmetrical inhibitory-excitatory-inhibitory responses (CI = inhibitory-excitatory-inhibitory; CII = excitatory-inhibitory-excitatory) (D) Purely excitatory responses.

Recordings were also made from the lateral geniculate nucleus. These responses were very similar to type A (on-centre neurones), type B (off-centre neurones) or the types CI and CII.

From a comparison of intracellular with extracellular recordings at the cortical level differences were noted in the responses of directionally selective neurones to movement in the null direction. In extracellular recordings these were essentially inhibitory. In intracellular recordings only one

case of a purely hyperpolarizing response was seen in the null
direction; sub-threshold epsps could usually be seen and
these were clearly antagonized by concomitant ipsps.
Innocenti and Fiore (1974) concluded that inhibitory responses
revealed by monocular conditioning, though already present in
the LGN, do reflect intracortical inhibition. However, they
argued that the inhibitory components of the receptive field
of geniculate cells are reconstructed at the cortical level by
a local mechanism (Watanabe, Konishi and Creutzfeldt, 1966).
Innocenti and Fiore (1974) qualified this statement by saying
that it is difficult to assess quantitatively the contribution
of intracortical inhibition and of thalamic disfacilitation to
the discharge suppression around the excitatory centre of the
cortical cell.

The role of the inhibitory sidebands in mediating
orientation tuning would suggest that cells lacking this
feature would lack orientation tuning. Bishop and Henry
(1972) themselves described simple cells with a single
side-band located to one side of the central discharge zone
and others with no sidebands yet showing orientation tuning.
One would predict, as Henry, Dreher and Bishop, (1974) and
Rose noted (Rose, 1977), that if sidebands were responsible
for the cell's orientation properties inhibition would be
shown for a stationary flashed bar as well as for a moving
bar. However, Bishop, Dreher and Henry (1972) and Bishop,
Goodwin and Henry (1973) found, when the inhibitory sidebands
were stimulated with stationary stimuli, excitatory responses
were frequently obtained at "on" or "off" at different sites
in the sidebands.

There is no evidence for a spatial division of the simple cell receptive field such that the extension of inhibition outside the central discharge zone constitutes a separate intracortical input mediating tonic inhibition and conferring on the cell its orientation properties. The dynamic properties of that inhibitory zone suggest a functional continuity with inhibition distributed within the central discharge zone. There is therefore a possibility that the tuning properties of the simple cell can be accounted for by the mechanism proposed for direction selectivity (Goodwin and Henry, 1975).

Goodwin and Henry (1975) argued for inhibition preceding stimulus motion on the basis of the absence of response in the non-preferred direction and of the absence of reduction in direction selectivity when stimulus speed is reduced. Though many neurones show direction selectivity (Schiller, Finlay and Volman, 1976a; Hammond, 1978) a large number show varied degrees of response in the non-preferred direction; they are direction biased (e.g. Hammond, 1978). Contrary to Goodwin et al's studies (Goodwin, Henry and Bishop, 1975; Goodwin and Henry, 1975) later studies have indicated that reduction in stimulus velocity is accompanied by reduced direction selectivity (Orban, Kennedy and Maes, 1981; Nothdurft, 1983). There is, however, evidence that direction-selective inhibition may be initiated by a stationary edge. Ganz and Felder (1984) investigated the direction selective properties within excitatory "on" or "excitatory "off" components of the receptive fields of direction-selective simple cells (a sub-group of simple cells whose direction selectivity is not a

product of synergistic action between "on" and "off" areas).
The direction-selective inhibition produced by pairs of
flashed bars with zero or small (0-25 milliseconds) temporal
asynchronies was equivalent to that for a bar moving across
the same receptive field positions.

2.4 The Mediation of Orientation and Direction Selectivities by Separate Mechanisms.

Schiller, Finlay and Volman (1976b, e) advanced four
arguments for the mediation of orientation and direction
selectivities by separate mechanisms.

(1) In the monkey, orientation preference is organized in a
columnar manner (Hubel and Wiesel, 1972, 1974) but cells of
the same orientation column may differ in their preferred
direction, with cells successively recorded showing opposite
preferred directions.

(2) Cells which show orientation selectivity with oriented
moving contrast bars show orientation selectivity when the
same stimulus is held stationary and flashed; orientation
tuning is not therefore contingent on stimulus motion.

(3) From their comparison of orientation and direction tuning
for moving bar and spot stimuli, Schiller, Finlay and Volman
(1976b) inferred that orientation tuning is critically
dependent on, and direction selectivity independent of,
stimulus length.

(4) If there is a dependent relationship between direction
selectivity and orientation selectivity it would be expected
that selectivity for orientation of directional cells
(Schiller's term) would be different from those of

non-directional ones. An evaluation was made for simple and complex cells separately. Schiller, Finlay and Volman (1976b) interpreted their data to show that the two groups, directional and non-directional cells, did not differ in terms of their orientation tuning, though the data were more complete for complex than simple cells, reflecting the predominantly unidirectional population in the simple cell group.

Schiller, Finlay and Volman (1976b) suggested that orientation and direction selectivities are accomplished by relatively independent mechanisms which appear to be linked since "directionality", by which is presumably meant preferred direction, is typically at right angles to the axis of orientation. Subsequent studies have yielded only partial support for Schiller's evidence.

The cortical organization of direction selectivity has received little attention. Payne, Berman and Murphy (1980) assessed the differences in preferred directions of cells within 200 microns of each other during tangential penetrations. They concluded that, compared with a random population, a significantly higher number of pairs had similar preferred direction preferences than opposite direction preferences. Tolhurst, Dean and Thompson, (1981) evaluated both the vertical and tangential organization of direction preferences, again with contrast bars. It was suggested that preferred direction is organized in an identical columnar fashion to orientation. In oblique penetrations, the correlation between preferred orientation and preferred

direction of pairs of neurones declined with increasing distance and was hardly evident at 300 microns. In normal penetrations, the measures declined together but a statistically significant correlation was retained up to 600 microns.

This study may be criticized on two counts. The preferred direction for a moving contrast bar is necessarilly orthogonal to orientation (Henry, Dreher and Bishop, 1974). That the correlation between direction and orientation declines at a faster rate in the horizontal than the vertical dimension can be seen as a consequence of the cortical organization of orientation. Secondly, if direction and orientation are organized on an identical columnar basis neither the absolute decline in correlation of preferred orientation with depth nor the relative decline in correlation between orientation and direction with increasing distance would be expected. Tolhurst, Dean and Thompson (1981) themselves observed a minority of neurones within the same orientation column which exhibited differences in preferred direction.

Schiller's observation that successively recorded neurones in vertical penetrations may show opposite preferred directions had previously been noted by Creutzfeldt, Innocenti and Brooks (1974) and confirmed by Hammond (1978). In this context Hammond's (1978) consideration of the columnar organization of bar and texture tuning is interesting. This clearly indicated that the direction and orientation mechanisms are not in register for all cells, especially those

of the infragranular layers. Differences in directional
tuning for bar and noise stimuli tended to be reflected in
sequences of consecutively recorded cells in a single
penetration, often over several hundred micra of electrode
advance. In that study, three neurones, presumed to be
cortico-tectal neurones, were recorded successively in a
single penetration and, although the preferred direction for
the first recorded cell was exactly the opposite to that for
the remaining two, the cell showed similar differences between
preferred directions for bar and noise. In addition, abrupt
changes in texture tuning, even between neighbouring cells
with similar preferred orientations for a bar, were seen.
There is therefore confirmation that cells which show similar
preferred orientations may have different directional tuning
properties.

A supporter of Bishop's model might raise the objection
to Schiller, Finlay and Volman's (1976b, e) second argument
that if tuning for stationary and moving bars were seen to be
identical this would show that inhibition mediating the
response to a moving bar could be identical to that producing
the stationary bar response.

Schiller's model, like Bishop's, assumes that the
preferred direction for a spot is identical to that for a
moving bar. Equally it would require that the bar is a linear
sum of spots with each position within the bar given an equal
weighting function. There is evidence that the latter
assumption is not valid (Bodis-Wollner, Pollen and Ronner,
1976; Rose, 1977; Hammond and Andrews, 1978a, c) as is

discussed further (chapter three). Indeed, there is some evidence that preferred orientations/directions for forward and backward motion of contrast bars are not identical (Albus, 1975; Hammond, 1978c). Many neurones are unresponsive to spots (Henry, Bishop and Dreher, 1974; Rose, 1977).

Comparing orientation tuning for direction selective and non-selective neurones, Schiller, Finley and Volman (1976b) found no dependent relationship between orientation tuning and the degree of direction selectivity. Evidence to the contrary for complex cells has been given by Harvey (1980). A population of 18 cortico-tectal, special and standard complex cells was compared. Of the ten complex cells which showed little or no length summation, all were highly selective for direction of stimulus motion. But, of the eight cells which responded optimally to long edges, four showed no direction selectivity and two were weakly direction selective, direction selectivity being defined in relation to preferred and non-preferred directions.

Results from pharmacological and deprivation studies are compatible with the mediation of orientation and direction selectivities by separate mechanisms. For example, Sillito (1975b, 1977) found that, for complex cells of the infragranular layers, orientation selectivity but not direction selectivity was considerably reduced following the iontophoretic application of bicuculline. Several studies have shown that selective exposure, during the critical period, to a stroboscopically illuminated environment - which deprives the kittens of real visual movement - results in

cortical neurones which display orientation selectivity but whose direction selectivity is lost (Cynader, Berman and Hein, 1973; Olson and Pettigrew, 1974; Cynader, Berman and Hein, 1975).

The most direct evidence for the mediation of orientation and direction selectivity by separate mechanisms comes from the extensive studies of the tuning properties of complex cells for moving contrast bars and texture fields (Groos, Hammond and Mackay, 1976; Hammond and Mackay, 1977; Hammond 1978; Hammond 1979b, c; Hammond and Reck, 1980a, b). Comparisons of tuning for fields of moving visual noise and contrast bars against the same stationary noise field as background reveal a separation of peak positions of the tuning curves for the two stimuli which, in the case of cells showing a unimodal peak in the texture tuning curve, averages 30-40 deg. (Groos, Hammond and MacKay, 1976; Hammond and MacKay, 1977; Hammond, 1978). The difference is greatest for cells of the infragranular layers (Hammond, 1978) which show greater responsiveness to texture motion than those of the supragranular layers (Hammond and MacKay, 1977; Hammond, 1978).

Tuning for bar and texture motion differs in other respects. Optimal velocity and bandwidth are invariably higher for texture than bar motion (Hammond, 1978; Hammond and Reck, 1980a, b). Texture tuning is dependent on and bar tuning independent of velocity. At low velocities, texture tuning is unimodal but, at higher velocities, the tuning curve becomes bimodal with depression of response for directions

optimal for bar motion (Hammond and Reck, 1980a, b). However, some cells retain a unimodal response as stimulus velocity increases (Hammond and Reck, 1980a, b; Hammond and Smith, 1983).

Several lines of evidence indicate separate inputs mediating bar and texture sensitivity, in particular, interocular comparisons of tuning for these stimuli (Hammond and MacKay, 1977; Hammond, 1978; 1979b, c). At the cell's optimal velocity for a moving bar, ocular dominance for bar and texture may be similar or differ significantly for the two stimuli (Hammond, 1979; 1981b). Differences of up to three ocular dominance groups, with reversal of eye preference have been reported (Hammond, 1979b, c; 1981b). Binocular comparisons further indicate that velocity characteristics are not invariably identical for the two eyes (Hammond, 1981b). This study indicated that preferred direction for bars is velocity invariant through each eye although differences in width of bar tuning were sometimes seen. Only when preferred velocity and velocity bandpass differed between the two eyes did measured ocular dominance vary significantly with velocity. As with bar tuning, interocular differences in texture responsiveness and tuning at different velocities were also found to influence ocular dominance.

Collectively, the evidence from comparisons of tuning for moving bar and texture fields establishes that orientation and direction tuning are mediated by separate mechanisms associated with distinct inputs mediating bar and texture sensitivity. In one variant of Schiller's model (Schiller,

Finlay and Volman, 1976e) separate inputs were served by
parallel afferent fibre streams from the LGN to sites
associated with separate levels of inhibition. An immediate
question is raised of whether inputs mediating the orientation
and direction properties of cortical cells arise from parallel
streams from the lateral geniculate nucleus. A further
consideration is the role of the afferent input in determining
the temporal properties of tuning; Schiller's model suggested
the simple cell to be the recipient of both X and Y cell input
while in Bishop's model the simple cell receives only X fibre
input. As raised by Mason (1976), Ahmed (1981) and Ahmed and
Hammond (1984), the differential responsiveness of simple and
complex cells to visual noise could reflect differential input
from the LGN. The afferent input to simple and complex cells
is considered in these contexts.

2.5 X and Y Cell Input to Simple and Complex Cells

At lower levels in the retino-striate pathway, a number
of tests have been used to distinguish between X and Y cells.
A primary difference lies in linearity of summation; X and Y
cells differ in response to contrast reversal of a stationary,
sinusoidal grating. For X cells, a null position is seen
where no response is elicited but, for Y cells, contrast
reversal produces excitation at all parts of the receptive
field (Enroth-Cugell and Robson, 1966; Hamasaki and Sukea,
1979). X and Y cells differ in the time course of their
responses to a standing contrast, with X cells producing a
sustained response and Y cells a transient response (Cleland,
Dubin and Levick, 1971; Fukada, 1971). To a moving grating,

X cells show modulated responses for the full range of spatial
frequencies to which they respond whereas Y cells no
modulation at higher spatial frequencies (Cleland, Dubin and
Levick, 1971).

X and Y cells can be distinguished by other properties.
Receptive field sizes of X and Y cells are significantly
different (Hoffmann, Stone and Sherman, 1972; Cleland and
Levick, 1974; Hammond, 1974). Within the central 15 degrees
of the visual field, receptive field diameters of X cells
range from 0.5 to 1.5 degrees while those of Y cells range
between 1 and 4 degrees (Hoffmann, Stone and Sherman, 1972).
Cleland and Levick (1974) reported brisk-sustained units had
smaller receptive field centres than brisk-transient units
over the first 12 degrees from the area centralis. Hammond
(1974) documented differences between sustained on- and
off-centre and transient on- and off-centre cells in the
dimensions of the major axis of their receptive field centres,
the means being: sustained on-centre 1.30 degrees; sustained
off-centre 1.95; transient on-centre 2.30 degrees; and
transient off-centre 2.90 degrees, for units within seventeen
degrees of the area centralis.

X and Y cells differ in flicker sensitivity. Fukada and
Saito (1971) have reported differences in the responses of
Type I (Y cells) and Type II (X cells) ganglion cells to small
spots flickering in the receptive field centre. For Type I
cells, average impulse frequency was found to vary as a
function of flicker frequency, whereas the responses of Type
II cells were independent of flicker frequency. For Type I

cells, impulse frequency increased to a maximum and decreased
as the flicker frequency was further increased but for Type II
cells, this was essentially constant as the flicker frequency
was further increased. Also, with flicker stimulation near
the point at which the maximum impulse frequency occured, Type
I cells were seen to discharge periodically at about 200
impulses/sec., this firing superimposing on the response to
individual flashes of flicker.

X and Y cells differ in their responses to movement of
stimuli outside the classical receptive field. A 'periphery
effect' has been described by McIlwain (1964). A small spot
of light was flashed continuously within the receptive field
centre of a retinal ganglion cell and the intensity of the
spot was reduced until it was subthreshold. A disc was then
moved in the periphery and was found to bring the field centre
above threshold for response to the flashing spot (McIlwain,
1964). The periphery effect is absent or weak in X cells, but
seen for nearly all Y cells (Barlow, Derrington, Harris and
Lennie, 1977; Derrington, Lennie and Wright, 1979).

The complexity of cortical neurones' receptive fields,
arising from intracortical circuitry, means that criteria for
distinguishing between X and Y cells at the geniculate level
can only be applied with caution when inferring afferent input
to simple and complex cells. For example, cortical neurones,
especially simple cells, may have little or no maintained
discharge (Pettigrew, Nikara and Bishop, 1968; Rose and
Blakemore, 1974) and their responses are more transient than
those of the LGN (Ikeda and Wright, 1975). Cortical cells do,

however, differ in their summation properties and linearity or
non-linearity of summation may be an indication of input from
X or Y cells. Potentially, afferent input can be inferred
from receptive field properties, e.g. velocity selectivity or
size, or from conduction velocities of afferents, from
correlations between fibre termination and stratification of
neurones and, most directly from simultaneous recordings from
fibres and recipient cells.

For simple cells, Movshon, Thompson and Tolhurst (1978a)
found that, in the responses to stationary gratings flickering
in different parts of the receptive field, most simple cells
showed linear spatial summation and gave modulated responses
to gratings moved steadily across the receptive field.
Andrews and Pollen (1979) also reported similar linear
summation for a majority of simple cells but noted a minority
showing non-linear summation and which gave an unmodulated
response to moving gratings. However, the non-linear cells
were not distinguished from linear cells by preferred spatial
frequency. Preferred spatial frequency would be expected to
be lower if the the non-linear cells were driven by Y cells.
Movshon, Thompson and Tolhurst (1978c) attributed the
responses of non-linear simple cells to intracortical
circuitry.

Ikeda and Wright (1975) distinguished two classes of
simple cells on the basis of the time courses of their
responses to the step onset of a stimulus. Transient units
were found to be insensitive to gratings moving slowly across
the receptive field and preferred gratings of lower spatial

frequency whereas sustained units were found to be quite sensitive to low temporal frequencies. From latency measurements to a visual stimulus, sustained units were found to have longer latencies than the transient units from which it was inferred that sustained simple cells receive an X input and transient simple cells a Y input. In the same study it was reported that among complex cells were cells receiving an X input or a Y input. The overall conclusion was that cells receive sustained or transient input independent of the simple/complex division.

Movshon, Thompson and Tolhurst (1978c) found cells resembling Ikeda and Wright's transient cells only in area 18 thereby questioning the existence of a transient simple cell population in area 17. Both Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c) made measurements of spatial frequency tuning of simple cells from which estimates of sub-regions were made. Ikeda and Wright (1975a) reported the smallest regions to be smaller than those found for Y cells in the LGN but both Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c) reported many simple cells having spatial frequency selectivities within the range of geniculate Y cells.

For complex cells, Movshon, Thompson and Tolhurst (1978b) reported pronounced non-linearities of spatial summation which were more marked than their non-linear simple cell population (Movshon, Thompson and Tolhurst, 1978a). Complex cells were seen to respond to gratings of low spatial frequency with modulated discharge but at higher spatial frequencies an

unmodulated elevation of discharge was found (see also Maffei and Fiorentini, 1973; Ikeda and Wright, 1975). Comparisons of spatial frequency tuning indicated no difference separating simple and complex cells (Movshon, Thompson and Tolhurst, 1978b). Hubel and Wiesel (1962) found that the most effective stimulus for some complex cells was as narrow as for some simple cells. This has also been reported by Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c). The result would indicate that some complex cells are the recipients of X cell input.

Circumstantial evidence that simple and complex cells receive different inputs is apparent in the correlation between receptive field size and preferred stimulus velocity. Cortical cells with small receptive fields prefer slow moving stimuli, whereas cells with large receptive fields prefer faster moving stimuli (Pettigrew, Nikara and Bishop, 1968; Dreher, Hoffmann and Stone, 1971; Sherman, Watkins and Wilson, 1976; Wilson and Sherman, 1976; Leventhal and Hirsch, 1978). However, there is no support for a bimodal distribution between simple and complex cells and it would be reasonable to conclude that within both the simple and complex cell groups receptive field size and velocity preference are related to X and Y cell input.

Two early studies of latencies to electrical stimulation indicated a separation of afferent input between simple and complex cells. Hoffmann and Stone (1971) made measurements of latency after electrical stimulation to optic chiasm or optic radiation and reported that none of the simple cells had

latencies consistent with Y input though some had latencies consistent with X input. Stone and Dreher (1973) confirmed the result. In their study, Hoffmann and Stone (1971) reported 30% of their complex cell sample could be activated with latencies consistent with a mono-synaptic Y input and Stone and Dreher (1973) reported a proportion of their complex cell sample receiving Y input but others had latencies indicating X input.

Subsequently, Singer, Tretter and Cynader (1975) reported 40% of their simple cell sample to be driven by fast i.e. Y cells. Bullier and Henry (1979a) found the bulk of their simple cell sample to be mono-synaptically activated, with half of them activated by Y fibres and half by X fibres (Bullier and Henry, 1979b). Also, Singer, Tretter and Cynader (1975) reported that although some 40% of their complex cell sample were activated by fast conducting afferents, units were found that had latencies consistent with activation by slow afferents (or fast afferents over more than one synapse). Bullier and Henry (1979b) found that although many complex cells appeared to be activated mono-synaptically by fast afferents, a large proportion of the same units received inputs routed through additional synapses (c.f. Singer, Tretter and Cynader, 1975).

The approach from latency studies is not without difficulties of interpretation. Many cortical cells project back to the LGN (Gilbert and Kelly, 1975; Gilbert, 1977) and can therefore be activated antidromically by electrical stimulation of the optic radiation. Antidromic activation

could be the cause of the short latency shown by some cells (Stone and Dreher, 1973; Bullier and Henry, 1979a). Also, there is a difficulty in interpreting whether a unit with long latency to electrical stimulation is activated via fast afferents through several synapses or via slow afferents through one or a few synapses.

While no conclusions can be made from direct comparisons of the laminae of termination of geniculate fibres and the distribution of cell bodies of simple and complex cells, indirect evidence from lamination has shed light on the question of connectivity of X and Y with simple and complex cells. Simple cells are not confined in layer IV to lamina IVc as would be expected if simple cells are only driven by X cells (Gilbert and Wiesel, 1979; Bullier and Henry, 1979c). Comparing receptive field sizes, Gilbert (1977) and Leventhal and Hirsch (1978) found simple cells in lamina VI had the largest fields and lamina IV the smallest. Simple cells in lamina IV ab have larger fields than those in IV c (Gilbert and Wiesel, 1979; Bullier and Henry, 1979c). Leventhal and Hirsch (1978) found simple cells in lamina VI were sensitive to higher stimulus velocities than their counterparts in lamina IV. These results could be interpreted to be consistent with Y input to simple cells in laminae IV ab and VI and X input to those in lamina IV c.

Direct evaluation of afferent input by simultaneous recording from cortical neurones and their afferent input has been attempted in three studies. Lee, Cleland and Creutzfeldt (1977) found that, for a sample of six simple cells, three

were each excited by an X fibre, two from a Y fibre and one was the recipient of both X and Y input. Tanaka (1983) reported that simple cells receive mostly X cell input with "special" complex cells receiving only Y input but "standard" complex cells receiving both X and Y fibre input. Henry, Mustari and Bullier (1983) have reported that B cells receive inputs from slowly conducting axons.

From this review the following conclusions can be drawn. Firstly, there is no evidence that X and Y cells provide independent, parallel streams to simple and complex cells respectively, but there is strong evidence that within both classes of cortical cells there are members which receive input from either type of fibre. Evidence for both X and Y cell input to the simple cell, suggested in the first variant of Schiller, Finlay and Volman's (1976b, e) model, is limited to one cell in Lee, Cleland and Creutzfeldt's (1977) study.

If simple and complex cells do not receive differential inputs from the lateral geniculate nucleus, it is unlikely that the differential sensitivity of simple and complex cells to moving visual noise arises from differences in thalamic input. Several studies suggest, more directly, that the differential sensitivity of simple and complex cells to texture motion must arise from intracortical circuitry.

At the retinal level, Ahmed (1981) and Ahmed and Hammond (1984) reported that responses of both brisk sustained and brisk transient cells are modulated by moving fields of visual noise, with response modulation dependent on receptive field

size and the configuration of the texture elements determining
the temporal properties of response. Mason (1976) found no
differential sensitivity to visual noise between brisk
sustained and brisk transient neurones of laminated lateral
geniculate nucleus and between these cells and brisk transient
neurones of the MIN. The texture sensitivity of W cells is
unknown.

There is further evidence that the differential
sensitivity to visual noise between simple and complex cells
must arise from intracortical circuitry. X and Y cells convey
the same information about deterministic (bar) and texture
stimuli (Hoffmann, Morrone and Reuter, 1980). If a bar is
moved in phase with a field of visual noise, simple cells have
thresholds 2-4 times lower than LGN neurones (thresholds being
defined by the signal to noise ratio when amplitude of
response to bar was equal to the peak response to noise in a
PSTH). When the bar is moved across the stationary noise
field, the thresholds of the simple cells are still a further
two times lower than the thresholds of X and Y cells,
indicating a mechanism, in addition to averaging, is required
(Hoffmann, Morrone and Reuter, 1980). Hoffmann, Morrone and
Reuter (1980) suggested the hypothesis of an unselective
suppression of response to noise present in the LGN input.
They further suggested that this inhibitory input is mediated
by infragranular complex cells. In the case of lamina IV
simple cells, inhibition may arise from lamina VI. There is
anatomical (Gilbert and Wiesel, 1979, 1981) and physiological
(Ferster and Lindstrom, 1983) evidence of a pathway from
lamina VI to IV contacting inhibitory interneurones (Hornung,

McGuire and Wiesel (1983).

2.6 The Role of Dendritic Morphology and Inputs from Inhibitory Interneurones in the Construction of the Receptive Field

Schiller, Finlay and Volman (1976e) suggested three possibilities for the neural substrate of receptive field organization mediating orientation and direction selectivities. The first alternative was that of an isomorphism between the spatial organization of the receptive field (see fig. 2.1) and the spatial distribution of the apical and basal dendrites; the apical dendrite would show a biolobed distribution and the basal dendrites would be skewed relative to the cell body. As a second alternative, Schiller, Finlay and Volman (1976e) suggested that the inhibitory components of the receptive field would be· reflected in the distribution of inhibitory connections on the dendritic fields, with dense connections to some sites and few connections with others. Thirdly, it was suggested by Schiller, Finlay and Volman (1976e) that the geometry of the interneurones' axons might determine the organization of the receptive field.

Those studies which have considered the relationship between dendritic morphology and receptive field structure have been limited to assessing if there is a correlation between dendritic orientation and the cell's stimulus orientation preference. This relationship has been considered in the studies of Coleman, Flood and Emerson (1981), Tieman and Hirsch (1982) and Martin and Whitteridge (1984). Coleman

et al (1981) investigated the effect of selective exposure to striped cylinders with vertical or horizontal stripes and Tieman and Hirsch (1982) the effect of selective exposure to vertical or horizontal lines on the shape of dendritic fields as seen in Golgi preparations.

Coleman et al (1981) were unable to find a relationship between the spatial arrangement of dendrites and stimulus orientation during the exposure period for spiny and non-spiny stellate neurones in lamina IV of kittens when only measures of dendritic macrostructure (the general orientation of an entire dendritic tree and the relative elongation of the dendritic tree) were considered. By contrast, measuring the Dendritic Angular Distribution (DAD - the angular location of dendritic segments relative to the major brain axes as a function of distance from the cell body) provided evidence of a correlation between dendritic distribution and stimulus orientation during exposure. In the tangential plane, for control kittens (experiencing no exposure) there was a peak in the number of intersections at 90 deg; this peak remaining for up to 80-90 microns from the cell body. Those kittens reared viewing vertically oriented stripes produced two peaks in the DAD, one prominent at 270 deg. and a smaller one at 90 deg. i.e. in the dorso-ventral axis, approximating the cortical representation of the horizontal visual axis. For kittens reared viewing horizontal stripes, no clear peaks were seen in the DAD but distributions of angular positions at 30-40 microns appeared to be quite different from the distributions seen closer to the cell body. Thus, overall, for control cats the distribution appeared to correlate with

the distribution closer to the cell body, for kittens raised viewing horizontal or vertical stripes dendritic orientation distant from the cell body was affected by selective exposure, but only for kittens reared viewing vertical stripes was dendritic orientation clearly related to stimulus orientation during selective exposure.

Tieman and Hirsch (1982) reported that, for kittens in a control group not experiencing selective exposure, dendritic fields of lamina III pyramidal cells were uniform in distribution while the distributions for lamina III pyramidal cells, of kittens experiencing selective exposure, were shifted, the shift in distributions being related to conditions of viewing. Dendritic orientation was measured by two indices following the plotting of dendritic orientations of cells with the aid of Sholl diagrams and converting the x, y co-ordinates of each intersection of a dendrite with a circle into polar co-ordinates, each intersection being represented by a vector with an angle and a radius. The two indices were; the proportion of vectors within 45 deg. of vertical in the visual field and the mean angle for each cell using vector addition.

For kittens raised viewing only vertical lines, the dendritic fields were oriented orthogonal to the representation of the vertical meridian and, for kittens raised viewing only horizontal lines, the dendritic fields were oriented parallel to the representation of the vertical meridian. The distribution of dendrites of lamina IV spiny stellate neurones were found to be unaffected by selective

exposure in Tieman and Hirsch's (1982) study. To account for this, these authors argued that while some neurones in striate cortex require early visual experience for the development of orientation, others do not, the studies of Leventhal and Hirsch (1977, 1980), Fregnac and Imbert (1978) and McCall, Leventhal, Tieman and Hirsch (1981) being cited in support of this view.

The support given by the studies of Coleman, Flood, Whitehead and Emerson (1981) and Tieman and Hirsch (1982) for an association between dendritic morphology and a cell's preferred orientation is weak. The studies disagree on the effect of selective exposure on lamina IV spiny stellate cells and, indeed, on the magnitude and direction of dendritic orientation of pyramidal neurones following selective exposure. Schiller, Finlay and Volman's (1976e) model required that the orientation of the dendritic field to be perpendicular to the cell's preferred orientation (c.f. Colonnier's model, described earlier, which required the orientation of the dendritic field to match the cell's preferred orientation). Tieman and Hirsch's (1982) data are in accord with Schiller, Finlay and Volman's (1976e) model. However, as Tieman and Hirsch (1982) themselves have pointed out, the orientation of dendrites orthogonal to stimulus orientation might not necessarilly be a reflection of a relationship between dendritic orientation and a cell's preferred stimulus orientation but a byproduct of a cell's direction-selective properties with the relationship to preferred orientation incidental and arising as a consequence of orientation being orthogonal to the direction of motion of

a long bar.

Martin and Whitteridge (1984) have raised a number of objections to both studies: a selective sampling of cells was undertaken; with the Golgi method there is no certainty that similar populations of cells in normal and selectively reared animals are similar; differences in morphology of cells sampled between control and selectively reared animals were apparent. A major weakness of both Coleman, Whitehead and Emerson (1981) and Tieman and Hirsch (1982) studies is that, in neither study, were the neurones' preferred orientations, assessed in tuning curves from single cell recordings, determined. In Martin and Whitteridge's (1984) study, the preferred orientations of single cells were obtained in unit cell recordings and then the cells were injected with horseradish peroxidase. Cells from all laminae in cat striate cortex, with the morphology of pyramidal, spiny and non-spiny stellate neurones were included. In the tangential plane, no correlation was found between the cells' preferred orientations and orientations of their dendritic trees. In sum, there is no convincing evidence for a dependence of a cell's orientation preference, defined in terms of stimulus selectivity, and a neurone's dendritic orientation. Additionally, one might add, given that cells with similar morphology may differ in synaptic connectivity (Davis and Sterling, 1979), an undue emphasis on dendritic morphology is unwarranted.

The dependence of the orientational and directional tuning properties of cortical neurones on GABA-mediated

inhibition (Sillito, 1975, 1977, 1979; Berardi, Kemp, Wilson and Sillito, 1980) requires a role for inhibitory interneurones in the formation of the receptive field structure mediating these properties. Identification of GABA as the synaptic transmitter of a specific class of neurone or with a particular synaptic site potentially would yield insight into the formation of receptive field structure determining orientational and directional tuning.

Both anatomical and neuropharmacological evidence has identified non-spiny stellate cells as inhibitory interneurones. Golgi-EM studies (combining Golgi staining with electron-microscopy) have demonstrated that symmetrical synapses derive from the axon terminals of non-pyramidal, aspinous neurones (LeVay, 1973; Parnavelas, Sullivan, Lieberman and Webster, 1977; Somogyi, ·1977; Peters and Fairen, 1978; DeFelipe and Fairen, 1981; Somogyi and Cowey, 1981). Through two neuropharmacological techniques, the uptake of 3HGABA applied locally (Hokfelt and Ljundhal, 1972; Chronwall and Wolff, 1978; Hamos, Davis and Sterling, 1981; Hendry and Jones, 1981; Somogyi, Cowey, Halasz and Freund, 1981; Somogyi, Freund, Halasz and Kisvarday, 1981) and immunocytochemical techniques employing antibodies to the GABA synthetic enzyme glutamic acid decarboxylase (Ribak, 1978; Hendrikson, Hunt and Wu, 1981), the synaptic transmitter GABA has come to be associated with smooth stellate cells.

From Golgi studies, several distinct morphological types of non-spiny stellate neurones have been described in close association with pyramidal cells: the basket cell (Cajal,

1911; Marin-Padilla, 1969, 1974; Hollander and Vanegas, 1981); the double-bouquet cell (Cajal, 1911; Colonnier, 1966; Szentagothai, 1973, 1975, 1978; Jones, 1975); and the chandelier cell (Cajal, 1911; Colonnier, 1966; Szentagothai, 1973, 1975, 1978; Jones, 1975). For the pyramidal cell, symmetrical synapses have been identified on the cell body (Colonnier, 1968; Peters and Kaiserman-Abramof, 1970; LeVay, 1973; Fairen, Peters and Saldanha, 1977; Parnavelas, Sullivan, Lieberman and Webster, 1977; Peters and Fairen, 1978); dendritic spines (Colonnier, 1968; Peters and Kaiserman-Abramof, 1969; Jones and Powell, 1970; LeVay, 1973); dendritic shafts (LeVay, 1973) and on the axon initial segment (Westrum, 1966; Palay, Sotelo, Peters and Orkand, 1968; Jones and Powell, 1970; Sloper, 1973; Sloper and Powell, 1979).The use of the Golgi/EM technique has led to an identification of the neurones from which inhibitory synapses on the pyramidal neurone derive.

Distributed in laminae II through V, basket cells have an axon which forms horizontally extended branches or archades, the branches giving off short twigs and tufts which pass round the cell bodies of adjacent neurones to contribute to pericellular baskets (Cajal, 1911; Marin-Padilla, 1969, 1974; Hollander and Vanegas, 1981). The formation of pericellular baskets around the cell body, as seen in Golgi pictures, has suggested basket cells selectively contact the perikarya of pyramidal neurones (Cajal, 1911; Marin-Padilla, 1969, 1974; Marin-Padilla and Stibitz, 1974; Szentagothai and Arbib, 1974; Szentagothai, 1975, 1978; Jones, 1975; Tombol, 1978; Peters and Regidor, 1981).

In studies using the combined Golgi/EM method, synaptic contact of basket cells with pyramidal cell bodies has been confirmed. Peters and Proskauer (1980) reported a close association between a multipolar smooth stellate cell and a laminar III pyramidal cell in rat striate cortex. Electron microscopy showed the axon terminal to form symmetric synapses with the cell body of the pyramidal cell. The equivalence of this neurone with the basket cell of cat and monkey striate cortex has been made by Peters and Regidor (1981). DeFelipe and Fairen (1982) reported basket cells in the superficial layers of the cat visual cortex forming symmetric synapses with the perikarya of pyramidal neurones. Somogyi, Kisvarday, Martin and Whitteridge (1983), using an HRP/EM preparation, described three large basket cells in cat striate cortex forming symmetric synapses with pyramidal cell perikarya. Martin, Somogyi and Whitteridge (1983), using an HRP/EM preparation, reported two basket cells contacting the cell bodies of pyramidal neurones via symmetric synapses in cat striate cortex.

Several studies have provided evidence for the formation of pericellular baskets by convergence of an indeterminate number of basket cells (Cajal, 1911; Marin-Padilla, 1969, 1974; Hollander and Vanegas, 1981). At the same time, there is evidence that individual basket cells may contribute to the pericellular basket through multiple synaptic contacts with the cell body. In their study, Peters and Proskauer (1980) reported, for one multipolar smooth stellate cell and a laminar III pyramidal cell in rat striate cortex, the axon terminal formed five symmetric synapses with the cell body.

Hollander and Vanegas (1981) described axons, thought to derive from basket cells, which made a large number of synaptic contacts on the soma of a pyramidal cell. DeFelipe and Fairen (1982) also reported that multiple synaptic contacts were made on the cell bodies of pyramidal cells by basket cells in laminae II and III of cat striate cortex. Martin, Somogyi and Whitteridge (1983) described four basket cells forming multiple synaptic contacts with cell bodies of pyramidal neurones in cat striate cortex.

A reconsideration of the specificity of connectivity of basket cells with the pyramidal cell body has been necessary in the light of several studies. Peters and Proskauer (1980) reported their smooth stellate cell to form symmetric contacts not only with the pyramidal cell body, but also one symmetric contact with the apical dendritic shaft and three with basal dendrites. The study confirmed an earlier demonstration that multipolar neurones form synapses with a variety of post-synaptic processes of pyramidal neurones, including dendritic shafts and perikarya (Peters and Fairen, 1978). DeFelipe and Fairen (1982) reported basket cells in the superficial layers of cat striate cortex make symmetric synapses with the perikarya, but also the proximal dendrites of pyramidal cells. Somogyi, Kisvarday, Martin and Whitteridge (1983) reported that while approximately one third of basket-pyramidal neurone contacts were on the soma, 20% of synapses were located on spines and the remainder on apical and basal dendrites. In their study, Martin, Somogyi and Whitteridge (1983) reported that 90% of axon terminals of large basket cells synapse with pyramidal cells; 40%

involving the cell bodies and 50% with apical and basal
dendrites, the remaining 10% of boutons encountered synapsing
with dendrites which could not be identified.

Double-bouquet cells, first described by Cajal (1911),
have axons which emerge from the main shaft of a descending
dendrite, or from the cell body, to form thin main collaterals
which descend in a radial direction and so traverse layers II
through V in a bundle 20 to 150 microns in diameter (Somogyi
and Cowey, 1981). A number of studies have described the
vertical axon bundles of double-bouquet cells as following the
apical dendrite of pyramidal cells (Cajal, 1911; Colonnier,
1966; Szentagothai, 1973, 1975, 1978; Jones, 1975)
suggesting these neurones provide synapses on the apical
dendritic spines, though, even on the basis of Golgi
preparations, this assumption was questioned (Valverde, 1978).
Using the Golgi/EM method, Somogyi and Cowey (1981) reported
that, for double-bouquet cells of lamina III of cat striate
cortex, 86.4% of boutons (from a total of of 66) formed
synapses with dendritic shafts, many of them belonging to
non-pyramidal cells, 9% with perikarya of non-pyramidal cells
and only 4.6% with spines. Somogyi and Cowey (1981) reported
that no pyramidal cell body or axon initial segment was among
the postsynaptic structures.

The chandelier cell was first described by Szentagothai
and Arbib (1974). These cells are found from lamina II
through V in cat striate cortex (Peters and Regidor, 1981).
The axon is distinctive, branching a short distance from its
origin to produce a plexus characterized by vertically

oriented branches composed of strings of bouton-like swellings
(Peters and Regidor, 1981). On the basis of the Golgi
picture, several authors suggested the apical dendrite of
pyramidal neurones to be the site of synaptic contact of
chandelier cells (Szentagothai and Arbib, 1974; Jones, 1975;
Szentagothai, 1975, 1978; Tombol, 1978). This suggestion has
been denied on the basis of combined Golgi/EM studies.
Somogyi (1977) described a type of interneurone in rat visual
cortex showing vertically arranged threaded boutons that
synapse specifically with the axon initial segment of
pyramidal cells. This axo-axonal neurone has been equated
with the chandelier neurone (Somogyi, 1979; Somogyi, Hodgson
and Smith, 1979). Subsequently, Fairen and Valverde (1980)
showed that the terminal formations of chandelier cells make
symmetric synapses upon the initial segments of pyramidal
neurones in cat striate cortex.

To understand the contribution of GABA-mediated inputs to
the formation of receptive field structure, a primary question
is whether GABA can be identified as the transmitter of a
specific class of non-spiny stellate neurone. There is
emerging evidence that the non-spiny neurones using GABA are
non-homogeneous.

Somogyi, Kisvarday, Martin and Whitteridge (1983)
advanced three lines of indirect evidence that basket cells
use GABA as a transmitter. Firstly, these authors noted that
the types of synaptic contacts formed by their sample of
basket cells, and the types of synaptic vesicles of boutons
seen in their study were the same as those of GAD

immunoreactive terminals in rat (Ribak, 1978), monkey (Ribak, Harris, Vaughn and Roberts, 1979) and cat (Freund, Martin, Smith and Somogyi, 1983). Secondly, Freund, Martin, Smith and Somogyi's (1983) study of boutons on lamina III pyramidal cells in cat striate cortex demonstrated that nearly all boutons on the perikarya and proximal dendrites are GAD positive therefore, they argued, the boutons of large basket cells in their study (Somogyi, Kisvarday, Martin and Whitteridge, 1983) provide inputs at sites which are very likely to be among the GAD-positive terminals. Thirdly, they argued, on the basis of the similarity in morphology between Martin, Somogyi and Whitteridge's (1983) basket cells and cells in Freund, Martin, Smith and Somogyi's (1983) study, which were shown to contain GAD, for an identity of these neurones with basket cells.

Ribak (1978) has characterized the axo-axonic synapse as using GABA since GAD-positive terminals make symmetric contacts on initial segments. The axo-axonic synapse is specific to the chandelier cell (Somogyi, 1977; Fairen and Valverde, 1980), thereby implicating the transmitter for the chandelier cell as GABA. Additionally, Somogyi and associates (Somogyi, Cowey, Halasz and Freund, 1981; Somogyi, Freund, Halasz and Zoltan, 1981) have provided evidence that the transmitter of the double-bouquet cell is GABA; 3H-GABA, injected into laminae V and VI of the primate visual cortex labelled, by selective retrograde transport, neurones within lamina II. The neurones were identified as double-bouquet cells which are known to have radially arranged axons travelling in bundles and terminating within lamina V (Somogyi

and Cowey, 1981).

It follows from the preceding review that GABA cannot be identified as the synaptic transmitter of a single class of non-spiny stellate neurone nor, given the diversity of sites of synaptic contact of basket, chandelier and double-bouquet cells, with a specific synaptic site on the pyramidal neurone. On the basis of connectivity patterns revealed in Golgi/EM and HRP/EM studies of basket, double-bouquet and chandelier cells (Somogyi, 1977; Fairen and Valverde, 1980; Somogyi and Cowey, 1981; DeFelipe and Fairen, 1982; Martin, Somogyi and Whitteridge, 1983; Somogyi, Martin, Kisvarday and Whitteridge, 1983), there is no support for Schiller, Finlay and Volman's (1976e) suggestion of two separate levels of inhibitory interneurones associated with apical and basal dendrites.

Schiller, Finlay and Volman's (1976e) model assumed representation of the simple cell by the pyramidal neurone. Lamina IV is a primary site in which simple cells are distributed (Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Hirsch, 1978) in which simple cells may be represented by spiny stellate neurones (Gilbert and Wiesel, 1979; 1981). The division of inhibitory synapses into two levels for the spiny stellate neurone would be unrealistic. If applicable, the model would be more appropriate for the complex cell, for which there is a good correlation with the pyramidal neurone (Kelly and Van Essen, 1974; Lin, Friedlander and Sherman, 1979). However, from the preceding discussion, it has been argued that Schiller, Finlay

and Volman's (1976e) assumptions about inhibitory inputs to
the pyramidal neurone are invalid.

The diversity of sites of different inhibitory
interneurones associated with the pyramidal neurone is
problematical in understanding which inhibitory input is
responsible for individual components of receptive field
structure and attributes of the cell's tuning properties.
Differences within the non-spiny stellate group, in terms of
specificity of site of synaptic contact, type of neurone
contacted and spatial extent of axonal arborization do suggest
diverse roles and, on the basis of connectivity and
morphology, one may ask how these differences are related to
function.

The selective and exclusive formation of an axo-axonic
synapse by the chandelier cell with the pyramidal neurone
(Somogyi, 1977; Fairen and Valverde, 1980) would suggest the
role of a gating neurone, specific to the pyramidal cell,
acting at the output stage (Colonnier, 1981). The
double-bouquet cell, contacting both non-pyramidal as well as
pyramidal cells shows a lower specificity compared with the
chandelier cell reflected in the synaptic contact with
dendritic shafts on non-pyramidal and pyramidal cells,
perikarya of non-pyramidal cells and spines (Somogyi and
Cowey, 1981). The axonal spread of the double-bouquet cells,
with axons arising from the main shaft of a descending
dendrite or cell body, to form collaterals which pass through
layers II to V in a bundle 20 to 150 microns in diameter
(Somogyi and Cowey, 1981) is relatively narrow. Thus, the

axonal spread is considerably more localised than the basket cell which may reach 700 microns (Gilbert and Wiesel, 1979, 1981). Inhibitory action would therefore be sharp, due to the limited axonal spread, but diverse in the synaptic location at which inhibition is effected.

The pyramidal cell, as Somogyi, Kisvarday, Martin and Whitteridge (1983) have argued, may receive inputs at three levels from basket cells: a generalised inhibition, via input to the soma, of excitation coming to the soma via the neurone's dendrites; selective inhibition of particular dendrites, mainly the apical dendrite; selective inhibition of excitatory input to particular parts of the dendrite. If the cell body provides the optimal site for an inhibitory input to the cell body (Jack, Noble and Tsien, 1975), but individual basket cells make relatively few contacts with the cell body (Somogyi, Kisvarday, Martin and Whitteridge, 1983), an important contribution to receptive field structure may arise from convergence of basket cells on the cell body (Somogyi, Kisvarday, Martin and Whitteridge, 1983). Thus, a complication to the understanding of the role of the basket cell arises from the multiple sites of contact with the pyramidal neurone and from the contribution of convergent inputs to the pericellular basket.

In considering the functional role of the basket cell, an important consideration has been the pattern of arborization seen in Golgi preparations. The view, based on the Golgi picture, that the basket cell might fulfil a role in the construction of orientation columns (Colonnier, 1966;

Marin-Padilla and Stibitz, 1974; Jones, 1975, 1981;
Szentagothai, 1973, 1975, 1978; Peters and Regidor, 1981) is
undermined by the absence of a correspondence between the
spatial distribution of axons with the shape or repetition
rate (Martin, Somogyi and Whitteridge, 1983) with the
dimensions suggested for orientation columns (Hubel and
Wiesel, 1963, 1974; Shatz, Lindstrom and Wiesel, 1977). The
slab-like appearance of the axonal arborization of the basket
cell in Golgi preparations (Marin-Padilla and Stibitz, 1974;
Jones, 1975; Peters and Regidor, 1981) would appear, on the
basis of Martin, Somogyi and Whitteridge's (1983) study, using
HRP-injected material, to underrepresent the axon arborization
of the basket cell.

The wide extent of the axonal arborization of the basket
cell could, potentially, mediate inhibitory interactions
across columns with dissimilar tuning properties. If
orientation-selective inhibition is generated by columns with
preferred orientations distant from that of the recipient cell
(Sillito, 1976, 1979), the basket cell would be a more
plausible candidate for mediating orientation-selective
inhibition than the double-bouquet cell with its more limited
horizontal axonal spread.

2.7 The Horizontal Organization of the Striate Cortex

Creutzfeldt, Kuhnt and Benevento (1974) held the view
that the lateral connections in striate cortex are inhibitory
and emphasised the functional role of inhibition at
orientations near the cell's preferred orientation.

Inhibition in Creutzfeldt's model is centred around the optimal orientation and arises from horizontal interactions extending little more than one orientation column. Creutzfeldt, Kuhnt and Benevento (1974) suggested inhibitory interactions between adjacent columns on the basis of intracellular recordings. Thus, these authors noted (Creutzfeldt, Kuhnt and Benevento, 1974) that;

"It is important to emphasise that inhibition within the excitatory region appears also during the response to the optimal stimulus, it is often better recognized under these optimal stimulus conditions than when the stimulus is oriented non-optimally. This may be partly due to the fact that IPSPs are relatively larger when the cell is depolarized but also indicates a true difference of inhibition at or near the optimal orientation."

The model was in line with psychophysical experiments in man showing mutual inhibition between detectors with slightly different orientations (Andrews, 1965; Blakemore, Carpenter and Georgeson, 1970). Also, Blakemore and Tobin (1972) demonstrated, in cat striate cortex, inhibition centred around the same orientation as the peak in the tuning curve for a moving contrast bar. Blakemore and Tobin (1972) established the preferred orientation for a cell and, while repeatedly stimulating the cell with that stimulus, moved a high contrast grating, covering the whole of the stimulus screen except for a circular area slightly larger than the cell's receptive field, at a range of orientations. Blakemore and Tobin (1972) reported the grating inhibited the cell's response over a broad range of orientations (-60 deg. to +60 deg. relative

to the cell's preferred orientation) centred at the same
orientation as the peak of the bar tuning curve. Inhibition,
in this context, was suppression of response below the cell's
resting discharge seen in extracellular recordings.

Axonal degeneration studies in monkey (Fisken, Garey and
Powell, 1973, 1975) and cat (Creutzfeldt, Garey, Kuroda and
Wolff, 1977) indicate extensive spread of horizontal fibres
(up to 4 mm in monkey and 1.5 mm in cat) compatible with
horizontal interactions extending between columns representing
all orientations (Hubel and Wiesel, 1974; Albus, 1975) and
encompassing receptive field centres of neurones over a visual
field area of 2-4 deg. depending on eccentricity
(Creutzfeldt, Innocenti and Brooks, 1974; Albus, 1975). The
rate of fall-off in the relative numbers of asymmetrical
terminals is much more rapid than that of symmetrical ones;
connections over long distances are inhibitory (Fisken, Garey
and Powell, 1973) with the exception of interactions between
columns representing the same orientation (Mitchison and
Crick, 1982). For the monkey (Fiskin, Garey and Powell, 1973,
1975) and the cat (Creutzfeldt, Garey, Kuroda and Wolff,
1977), an asymmetry in the spread of horizontal connections is
seen, as suggested by intracellular recordings (Benevento,
Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and
Benevento, 1974) and required by Creutzfeldt's model
(Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt
and Benevento, 1974). The asymmetry is more conspicuous for
the oblique than the short horizontal fibres in the cat
(Creutzfeldt, Garey, Kuroda and Wolff, 1977).

Pharmacological studies have confirmed inhibitory interactions from columns representing orientations distant from that of the recipient column (Hess, Negishi and Creutzfeldt, 1975; Hess, Ostendorf, Sanides, Negishi and Creutzfeldt, 1976) and have revealed the relative contributions of inhibition from columns far and close to the recipient column (Sillito, 1976, 1978). In the two studies by Hess and co-workers, inhibitory interactions were seen to extend laterally 400 microns, with a maximal effect between 100 and 200 microns. Inhibitory interactions between adjacent neurones cannot be ruled out (Hess, Negishi and Creutzfeldt, 1975) and are suggested by results of double recordings from a single electrode (Creutzfeldt, Kuhnt and Benevento, 1974; Hess and Murata, 1974) and the cross-correlation study of Toyama, Kimura and Tanaka, 1981a, b).

Sillito (1976), commenting on the broadening of the complex cell orientation tuning curve following iontophoretic application of bicuculline, inferred that inhibition acting in the orientation domain would be generated by orientations up to 90 deg. from the cell's optimum. Later, in a quantitative evaluation of GABA-mediated inhibition, Sillito (1978) compared normal orientation tuning curves for moving contrast bars with those observed during the iontophoretic application of bicuculline, thereby providing a basis for estimating the orientation tuning of GABA-mediated inhibition. It was concluded that, at normal resting discharges, orientations to either side of the optimal orientation, rather than those centred at the optimum, generate the most powerful inhibitory input. Thus, neurones in the striate cortex receive

inhibitory inputs via intracortical pathways which are anisotropically organized with maximal inhibition provided by neurones with preferred orientations distant from that of the recipient cell.

2.8 The Vertical Organization of the Striate Cortex

In the models of Bishop, Coombs and Henry (1971b), Goodwin and Henry (1975) and Schiller, Finlay and Volman (1976a), complex cells were assumed to derive their orientation and/or direction selectivities from simple cells. Pharmacological studies have shown that some complex cells derive their orientation or direction selectivities from a tuned, excitatory input (Sillito, 1975, 1976a, b, 1977, 1979). These studies do not, however, identify the receptive field class of the cells providing that tuned input. In the following section, consideration is given to the patterns of intracortical pathways, demonstrated by anatomical and physiological methods, through which excitatory connections are formed.

By reference to physiological studies, the questions of whether and how simple and complex cells are functionally linked by excitatory connections is discussed. Additionally, the possibility that some complex cells may derive some of their properties from other complex cells is considered. In providing the bridge between anatomical and physiological studies, it is assumed that complex cells are represented morphologically by pyramidal neurones (Kelly and Van Essen, 1974; Lin, Friedlander and Sherman, 1979; Gilbert and Wiesel

1979, 1981) though, since some complex cells may be
represented morphologically by non-spiny or partially spiny
stellate neurones (Martin, Somogyi and Whitteridge, 1983),
this is an oversimplification.

2.8a Intracortical Circuitry Revealed by Anatomical Methods

Excitatory connections are formed by pyramidal and spiny
stellate neurones (LeVay, 1973; Peters and Fairen, 1978;
Somogyi, 1978; White, 1981; Peters and Kimurer, 1981;
Peters and Proskauer, 1980a, b, 1981). Spiny stellate
neurones show localised dendritic and axonal spread,
suggesting they receive afferent input and form localised
connections in the lamina in which the cell bodies are
distributed (Cajal, 1922; O'Leary, 1941; Lorente de No,
1949; LeVay, 1973; Szentagothai, 1973; Fairen and Valverde,
1979; Lund, Henry and Harvey, 1979). From the distribution
of apical and basal dendrites, pyramidal cells are
functionally linked to laminae outside the layer in which the
cell body is located (Lund and Boothe, 1975; Lund, Henry and
Harvey, 1979). Axons of pyramidal cells in laminae II to VI
project extrinsically with supragranular layer pyramidal cells
sending axon collaterals to lamina V (O'Leary, 1949; Lund,
Henry and Harvey, 1979).

Spiny stellate neurones are prominently distributed in
lamina IV (Cajal, 1922; O'Leary, 1941; LeVay, 1973;
Szentagothai, 1973; Lund, Henry and Harvey, 1979; Fairen and
Valverde, 1979). Axons spread locally, those of lower lamina
IV spread laterally in the upper part of lamina IV and those

of the upper part of lamina IV have long horizontal branches which give off vertically oriented collaterals extending into lamina II and III (Lund, Henry and Harvey, 1979; Gilbert and Wiesel, 1979; Peters and Regidor, 1981). LeVay (1973), using the Golgi/EM method, reported the recipient cell post-synaptic to spiny stellate cells of lamina IV to be pyramidal cells. The distribution, synaptology and connectivity of spiny stellate cells suggests they form the source of excitatory pathways arising from lamina IV.

Pyramidal neurones occupying the middle to lower regions of lamina IV are few (Lund, Henry and Harvey, 1979) but the border of lamina IVa/III is populated by large pyramidal neurones (O'Leary, 1941; Lund, Henry and Harvey, 1979) those of upper lamina IV resembling adjacent stellate cells except for the possession of an apical dendrite. The border pyramids (O'Leary, 1941) of lamina IVa/III have an apical dendrite which branches just superficially to the cell body and extends to reach lamina II or I with occassional branches in lamina III or II (Lund, Henry and Harvey, 1979; Lorente de No, 1949). The axons of these neurones have collaterals rising obliquely to lamina III and II and others that run laterally within lamina IV and the descending trunk contributes to lamina V and continues out of the cortex.

Pyramidal cells of the infragranular layers differ in the extent of arborization of the apical dendrite (Cajal, 1911, 1922; Lorente de No, 1949; O'Leary, 1941; Lund, Henry and Harvey, 1979). Apical dendrites of lamina V pyramidal cells show side branching of the apical dendrite close to the soma

then the dendrite ascends with few or no side branches frequently reaching lamina I (Lund, Henry and Harvey, 1979). Basal dendrites arborize mainly within lamina Va though Lund, Henry and Harvey (1979) reported some spread to lamina Vb and the lowest part of lamina IV. The axon largely parallels that of the basal dendrites (Lund, Henry and Harvey, 1979). Apical dendrites of lamina Vb traverse the superficial laminae reaching lamina I and their axons give off collaterals in lamina Vb before projecting out of the cortex. The majority of lamina VI pyramids have apical dendrites which arborize in laminae VI and V then ascend to lamina I with minimal branching in laminae IV, III and II (Lund, Henry and Harvey, 1979). The specific arborization of lamina VI pyramidal apical dendrites found in the monkey (Lund and Boothe, 1975) is absent in the cat (Lund, Henry and Harvey, 1979).

Axonal degeneration complements the Golgi method but overcomes two limitations of the latter; that it is difficult to make generalizations from individual neurones and axons cannot easily be traced over long distances. Axonal degeneration has been used in the striate cortex of the cat by Creutfeldt, Garey, Kuroda and Wolff (1977) and in the monkey by Spatz, Tigges and Tigges (1970), Fisken, Garey and Powell (1973, 1975) and Tigges, Spatz and Tigges (1973). Each study used intact cortex but the study of Creutzfeldt, Garey, Kuroda and Wolff (1977) additionally used chronically isolated cortex, thereby enabling them to distinguish between degenerating fibres of extrinsic and intrinsic origin. The distribution of fibres seen in chronically isolated and intact cortex were similar.

Creutzfeldt, Garey, Kuroda and Wolff (1977) identified four fibre systems following intracortical lesions: (a) vertically descending; (b) obliquely descending; (c) obliquely ascending; and (d) horizontal fibres. No significant vertically upwards coursing group of fibres was seen. Horizontal fibres were found in considerable numbers for approximately 500 microns from lesions mainly in laminae I, III, IV and V, a few reaching 2-3mm. Oblique axons were seen to run downwards from the middle layers into laminae V and VI or upwards into laminae I and II. Axons arising from laminae II to V were seen to descend vertically into the white matter. Additionally, Creutzfeldt, Garey, Kuroda and Wolff (1977) found degeneration in lamina V, following superficial lesions, as had Fisken, Garey and Powell (1973, 1975) but their presence was described as moderate, contrasting with the massive degeneration in lamina V reported in the monkey by Spatz, Tigges and Tigges (1970) and Nauta, Butler and Jones (1973). In other respects, the pattern seen monkey is similar to that in cat (Spatz, Tigges and Tigges, 1970; Fisken, Garey and Powell, 1973, 1975; Tigges, Spatz and Tigges, 1973) though differences are seen in the extent of the axonal spread (Fisken, Garey and Powell 1973; Creutzfeldt, Garey, Kuroda and Wolff, 1977). Degeneration studies are therefore in agreement with Golgi studies in suggesting efferent pathways from laminae II to VI, intrinsic pathways arising from laminae IV, vertically ascending or descending, and an intracortical pathway from the supra- to the infragranular laminae.

2.8b Intracortical Connectivity Revealed by Physiological Techniques

Early intracellular studies indicated three patterns of connectivity to and within the striate cortex of the cat: monosynaptic excitation and disynaptic inhibition upon cortical cells of laminae III-V; disynaptic excitation and trisynaptic inhibition of cells of laminae III-V; and disynaptic excitation and trisynaptic inhibition on cells of laminae II and VI (Creutzfeldt and Ito, 1968; Ohno, Kiyohara and Simpson, 1970; Toyama, Matsunami, Ohno and Takashiki, 1974). The more recent study of Ferster and Lindstrom (1983) confirmed and extended these results. Laminae III, IV, upper V and VI were seen to be monosynaptically excited by geniculate afferents, while cells in laminae II and lower V were seen to receive only indirect excitation via other cortical neurones. Lamina III neurones were distinct in that they were found to receive a prominent excitatory input over two synapses in addition to direct excitation from the LGN. Identifying the receptive field structure of cells intracellularly recorded, Ferster and Lindstrom (1983) reported simple cells of lamina IV and VI to be monosynaptically innervated, while complex cells of laminae II, III, V and VI showed connectivity patterns related to their laminar patterns. Those in laminae VI and upper V received direct excitation, those in lamina III received direct plus indirect excitation and those in lamina II and lower V only indirect excitation from the LGN. For cells identified by their efferent projections, a pattern of connectivity was revealed in which cortico-geniculate neurones

are monosynaptically excited and cortico-collicular neurones di- and trisynaptically excited by geniculate afferents. Cortico-cortical neurones in laminae II and III were found to receive excitation over two synapses, or over one synapse plus excitation over two synapses, depending on laminar position (Ferster and Lindstrom, 1983). Ferster and Lindstrom (1983) also identified an excitatory pathway from lamina V to VI. Intracellular studies therefore indicate a diversity of connectivity patterns amongst complex cells with intracortical excitatory pathways contributing inputs to cells of both the supra- and infragranular layers.

Results from current-source-density analysis are in accord with anatomical studies in suggesting lamina IV to be the principal site for the origin of intracortical excitatory pathways (Mitzdorf and Singer, 1978). Three prominent excitatory pathways in cat striate cortex, each starting from lamina IV, were identified by these authors. The first would form an excitatory pathway to supragranular pyramidal cells via local connections to lamina III and from there, via long distance connections, to lamina II. A second pathway would link lamina IV to V, contacting the apical dendrites of lamina VI pyramidal neurones. The third pathway, with one synaptic delay in lamina IV, would provide an excitatory connections from lamina IV to III. In addition, current-source-density analysis (Mitzdorf and Singer, 1978) also indicated convergence of excitatory input from the supragranular layers to lamina V.

Consistent with simple cells forming the first link in

the excitatory pathways arising from lamina IV, it is known that simple cells are the predominant receptive field class in lamina IV (Hubel and Wiesel, 1962; Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Hirsch, 1978). By contrast, cross-correlation studies provide weak support for a functional link between simple and complex cells. Michalski, Gerstein, Czarkowski and Tarnecki (1983) made comparisons of response planes (Palmer and Davis, 1981) to determine whether the type of interaction between neurones depends on receptive field class. Response planes were analysed for twenty-four neurones; six pairs were recorded (at different times) with one bundle of electrodes and in four cases three neurone groups were studied, consisting of two neurones from one bundle and a third from the other bundle. The population consisted of seven simple cells and seventeen complex cells with interactions between complex cells reported for ten pairs; three pairs where both were simple and five cases where one cell was simple and the other complex. Eight out of ten interactions between complex cells revealed shared input and two were stimulus dependent. For the three pairs of simple cells, one pair shared input co-ordination, one was stimulus dependent and one did not show any co-ordination. The simple/complex pairs had shared interactions in three out of five cases, stimulus-dependent in one case and both stimulus dependent and direct excitation in only one case.

Toyama, Kimura and Tanaka's (1981a, b) study, described earlier, provided data on a much larger sample of neurones. That study and Michalski, Gerstein, Czarkowska and Tarnecki's (1983) are in agreement in reporting that shared input is the

most common form of co-ordination and includes a broad range of receptive field types. However, Toyama, Kimura and Tanaka (1981a, b) had reported direct connections only between complex cells or from complex cells to hypercomplex cells. Michalski, Gerstein, Czarkowska and Tarnecki's (1983) demonstration of a direct connection, simple to complex, needs to be treated with caution since this was shown for only one cell and for that example it was combined with a large stimulus peak making the correlogram difficult to interpret.

Even if simple cells provide an input to complex cells, there is evidence against the view (Henry, Dreher and Bishop, 1974; Goodwin and Henry, 1975 and Schiller, Finlay and Volman, 1976a) that the orientation and direction tuning of complex cells in the supragranular layers derives from an input from lamina IV. Malpeli (1983) has studied the effect of functionally inactivating cortical laminae by selective injection of 4mM cobaltous chloride into lamina A of the lateral geniculate nucleus. Following the injection, visual activity in laminae IVab, IVc and VI was virtually abolished. However, the orientation and direction selectivity of cells in laminae II and III was unaffected. In contrast, more variable effects were seen for cells in lamina V; special complex cells were least affected and simple cells the most.

Several studies, in addition to the cross-correlation study of Toyama, Kimura and Tanaka (1981a, b) suggest that some properties of complex cells may arise from an input from other complex cells, though the contributions of such inputs to receptive field structure remains to be established.

Lamina II cells receive only indirect excitation from the LGN (Toyama, Mackawa and Takeda, 1977; Toyama, Kimura, Shida and Takeda, 1977; Ferster and Lindstrom, 1983). Toyama et al (Toyama, Mackawa and Takeda, 1977; Toyama, Kimura, Shida and Takeda, 1977) reported that lamina II complex cells shared temporal features of response with cells of the middle layers and, in terms of spatial features of their responses along the direction perpendicular to the preferred orientation, resembled complex cells of the middle layers. Gilbert and Wiesel's (1979, 1981) studies reported complex cells, pyramidal in morphology and located in the upper part of laminae II and III, the descending axons of which project extensively in lamina V in which simple cells are few (Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Hirsch, 1978). Also, Gilbert and Wiesel (1979, 1981) have reported specific patterns of connectivity of lamina V 'standard' and 'special' complex cells, a characteristic feature of standard complex cells being an extensive projection to lamina VI, in which complex cells are invariably 'standard' (Gilbert, 1977; Gilbert and Wiesel, 1979, 1981) while 'special' complex cells send a large trunk out of the cortex to the superior colliculus (Gilbert and Wiesel, 1979, 1981). The laminar V to VI pathway, apparent also in the study of Ferster and Lindstrom (1983), would therefore appear to link complex cells with similar summatory behaviour.

The following conclusions may be drawn from this review of intracortical circuitry. Anatomical and physiological studies are in accord in suggesting multiple inputs to complex

cells some of which are of intracortical origin. The
diversity of connectivity patterns of complex cells seen in
anatomical and physiological studies is supportive of evidence
from pharmacological studies (Sillito, 1975, 1976a, b, 1977,
1979) of differences in the origin of tuning properties
between complex cells with some complex cells deriving their
orientation or direction tuning properties from an
intracortical excitatory input.

The contribution of intracortical excitatory pathways to
the receptive field structure of complex cells remains, at
best, poorly understood. A discrepancy exists between
cross-correlation studies, which provide little evidence of
excitatory connections between simple and complex cells, and
evidence that lamina IV, in which the simple cell
predominates, is a primary source of intracortical excitatory
pathways. The discrepancy may, in part, reflect the technical
difficulties of the cross-correlation technique.

If simple cells provide an excitatory input to complex
cells, the contribution of such inputs to the receptive field
structure of complex cells remains unclear. Malpeli's (1983)
study casts doubt on the assumption that lamina IV simple
cells provide the source of orientation and direction tuning
of supragranular complex cells or, indeed, lamina V 'special'
complex cells. Emerging evidence suggests a role for
excitatory connections between complex cells in the formation
of complex cell receptive field structure; pathways from
laminae III to II, from V to VI and III to V are suggested as
mediating such links. The latter pathway, as suggested by

Hammond and Reck (1980b), may provide the basis for the
greater sensitivity to texture motion of infragranular,
compared with supragranular, complex cells.

2.9 SYNTHESIS.

The primary objective of the preceding discussion has
been to establish the dependence of striate cortical neurones'
orientation and direction selectivities on intracortical
inhibition and the mediation of orientation and direction
selectivities by separate mechanisms. Consideration has been
given to the receptive field structure from which cortical
neurones' orientation and direction selectivities derive and
the underlying patterns of connectivity from which that
receptive field structure is built up.

The dependence of orientation and direction selectivities
on intracortical inhibition has been shown from the effects of
blockade of GABA-mediated inhibition and in the
orientation/direction dependence of intracortical inhibition
seen in intracellular recordings. Between simple and complex
cells, there is a differential dependence of orientation and
direction selectivities on intracortical inhibition with
simple cells showing a complete dependence on intracortical
inhibition.

Three models for the role of intracortical inhibition in
generating orientation and direction selectivities have been
reviewed. Bishop's model (Bishop, Coombs and Henry, 1971b)
assumed the key to understanding the tuning properties of

cortical cells to lie in the receptive field organization of the simple cell; specifically in the spatial relationship between intracortical inhibition and afferent excitation from the lateral geniculate nucleus. It has been argued that there is no separate component of the simple cell receptive field arising from tonic inhibition and conferring on the simple cell its orientation tuning; inhibition outside the central discharge zone shows a spatial and functional continuity with that within. From intracellular recordings, it has been demonstrated that the distribution of inhibition within the simple cell receptive field is not constrained by the spatial organization of excitatory input from the lateral geniculate nucleus. Inhibition throughout the receptive field has dynamic properties.

Afferent input from the lateral geniculate nucleus to the striate cortex is provided by parallel streams of X, Y and W fibres showing a laminar-specific pattern of projection. These parallel streams are not segregated at the geniculo-cortical synapse to produce parallel X fibre to simple cell and Y fibre to complex cell streams. Inhibitory input to the single cell comes from columns differing in preferred orientation with maximal contribution from columns distant from the recipient cell. As required by Creutzfeldt's model (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974), the pattern of fibres assumed to mediate inhibitory intercolumnar interactions is anisotropically organized.

Schiller, Finlay and Volman (1976e) suggested the

mediation of orientation and direction selectivities by separate mechanisms. Strong support for separate mechanisms mediating orientation and direction selectivities is given by studies showing dissimilar tuning for bar and texture motion. Comparisons of ocular dominance for moving contrast bars and fields of texture and velocity tuning for bar and texture motion have indicated bar and texture tuning to be associated with distinct inputs. Within the complex cell group, there are differences in the origin of bar tuning, some deriving their tuning properties from intracortical inhibition and others from a tuned excitatory input. At present, there is no strong evidence that simple cells provide the orientationally or directionally tuned input to these complex cells. Complex cells with similar summatory behaviour may differ in the origin of their orientation and direction tuning properties.

Current understanding of connectivity, at the single cell level, subserving these separate mechanisms is at a very early stage. A pre-condition for formulation of models for the neural substrate of these mechanisms is an appropriate model of receptive field structure. The model of Schiller, Finlay and Volman (1976b, e) incorporated an element of Bishop, Coombs and Henry's (1971b) model of simple cell receptive field structure; specificically, side-band inhibition. Therefore, the design was partly built on a false template. The models of Bishop, Coombs and Henry (1971b), Goodwin and Henry (1975) and Schiller, Finlay and Volman (1976b, e) made assumptions about the tuning properties of cortical neurones, and, by implication, receptive field structure, which were untested in the original formulations of the models; the

predictability of response to a moving bar from tuning for a stationary bar and linearity of summation.

The responsiveness of complex cells to texture motion imply a greater complexity of receptive field structure and connectivity than is required to explain bar tuning. The absence of a differential sensitivity to texture motion between the various classes of LGN cells requires an intracortical origin for the differential sensitivity to texture motion between complex and simple cells. Intracortical connectivity may also account for the greater texture sensitivity of complex cells in the infragranular layers compared with those in the supragranular layers.

Consideration is now turned to the tuning properties of simple and complex cells for contrast and textured stimuli. Studies which have evaluated tuning of simple and complex cells for contrast stimuli are reported and reviewed in the context of models for the role of intracortical inhibition in determining tuning characteristics. The tuning of complex cells for texture field motion is described to highlight differences in tuning properties and receptive field structure between complex and simple cells. Differences in tuning for contrast and textured stimuli between complex and simple cells are also considered as a background to a later discussion of how such differences suggest a distinct role for the complex cell in visual analysis.

CHAPTER THREE: THE TUNING OF SIMPLE AND COMPLEX CELLS FOR CONTRAST AND TEXTURED STIMULI

INTRODUCTION

Campbell, Cleland, Cooper and Enroth-Cugell (1968) provided the first quantitative study of orientation tuning properties of cortical neurones. Moving rectangular wave-form gratings were used to determine the relationship between response amplitude and orientation of the stimulus. A linear relationship between spike frequency and the angle on either side of the optimal or preferred orientation was reported, with linearity being maintained up to a point where response fell to zero or a base line frequency. The term angular selectivity was introduced and defined as the half-width at half-height of the tuning-curve. Angular selectivity of thirty-five neurones was determined and more than half of these fell within the range of 14-26 deg. Campbell et al noted that fourteen neurones were directionally selective, with twenty-one neurones producing a bi-directional response, though not of equal magnitude for opposite directions of motion. No significant correlation between response amplitude at optimal orientation and angular selectivity was found and the distribution of preferred orientation showed no bias for vertical/horizontal against oblique. In this study no distinction between cell types was made and data were combined from striate and extrastriate cortex.

3.1 The Form of the Tuning Curve for Moving Contrast Bars

The linear relationship found with gratings has also been reported for the tuning curve determined with moving contrast bars (Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Watkins and Berkley, 1974; Ikeda and Wright, 1975; Hammond and Andrews, 1978 a, b, c; Heggelund and Albus, 1978) and holds for simple, complex and hypercomplex cells (Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Hammond and Andrews, 1978 a, b) in cat striate cortex. Deviation from linearity has only been found at the extreme flanks of the tuning curve (Heggelund and Albus, 1978; Scobey and Gabor, 1979) with deviations from linearity significant only for broadly tuned units (DeValois, Yund and Hepler, 1982). There is some evidence that, for the monkey, the tuning curve follows an exponential function similar to the psychophysical curve for man (Campbell and Kulikowski, 1966; Campbell, Cleland, Cooper and Enroth-Cugell, 1968; Hubel and Wiesel, 1968). The shape of the tuning curve is invariant for a range of contrast values from three times threshold to threshold, though response amplitude is seen to decline with declining mean luminance (Bisti, Clement, Maffei and Meccacci, 1977). Constancy of tuning with changing mean luminance was also reported by Hoeppner (1974).

Though there has been some controversy over the question of time-dependent changes in orientation tuning, variability of tuning being reported by Horn and Hill (1969), Horn, Stechler and Hill (1972) and Donaldson and Nash (1973, 1975), the weight of evidence would indicate that though marked

spontaneous fluctuations in cells' responsiveness may occur
(e.g. Bishop, Coombs and Henry, 1971b; Lee, Cleland and
Creutzfeldt, 1977) orientation tuning assessed with moving
contrast bars remains constant (Hubel and Wiesel, 1962, 1965;
Barlow, Blakemore and Pettigrew, 1967; Pettigrew, Nikara and
Bishop, 1968; Hoffmann and Stone, 1971; Dreher, 1972;
Henry, Dreher and Bishop, 1974; Ikeda and Wright, 1974, 1975;
Andrews, Hammond and James, 1975; Hammond, Andrews and James,
1975).

3.2 The Tuning of Simple and Complex Cells for Moving Contrast Bars

For both simple and complex cells the tuning curves for
contrast bars of opposite polarity are identical (Henry,
Dreher and Bishop, 1974). Several studies have suggested
that, as a group, simple cells are more sharply tuned than
complex cells (Henry, Dreher and Bishop, 1974; Watkins and
Berkley, 1974; Albus, 1975; Hammond and Andrews, 1978 b;
Leventhal and Hirsch, 1978; DeValois, Yund and Hepler, 1982).
Henry, Dreher and Bishop (1974) reported the mean half-widths
for simple cells to be 17 deg. (range 8-31 deg.) compared
with 27.5 deg. (range 20.5-40 deg.) for complex cells.
Insufficient data were available for hypercomplex cells. Rose
and Blakemore (1974), though presenting no quantitative
analysis, observed sharper tuning for simple than complex
cells but no difference between these two groups and
hypercomplex cells. Heggelund and Albus (1978) found
differences in the mean orientation discrimination (MOD) - the
change in orientation angle away from the optimal which would

produce a response statistically different at the 1% level
from that at the optimum orientation - to be higher in simple
than complex cells. Sharper tuning for simple cells was
reported by Watkins and Berkley (1974) who, though finding
orientation tuning to be weakly related to receptive field
geometry, noted that cells with large fields are less
sensitive to stimulus orientation than those with small
fields. Hammond and Andrews (1978c) further confirmed
differences in tuning between simple and complex cells and
reported the relatively sharper tuning of simple cells in area
17 than in 18. In this study, average half-widths of tuning
in area 17 were reported to range from 7-50.5 deg. with a
mean of 18.3 deg. and a modal value between 10 and 15 deg.
Hammond and Andrews (1978b) found area 17 simple cells
half-width values to range from 7-26.5 deg. with a mean of
15.3 deg. and a modal value of 10-15 deg. Corresponding
values for complex cells were range 16.5-50.5 deg., mean 26.6
deg. and modal value 15-20 deg.

Comparison of tuning between simple and complex cells as
a function of eccentricity (Wilson and Sherman, 1976) and
laminar position (Gilbert, 1977; Leventhal and Hirsch, 1978)
have indicated class differences with relative constancy of
tuning for simple cells for each parameter. Wilson and
Sherman (1976) reported that the breadth of the orientation
tuning curve increased with eccentricity with a greater
eccentricity-related change in the orientation tuning of
complex than simple cells. These authors found the change in
receptive field size as a function of eccentricity to be more
evident for complex than simple cells. An increase in the

proportion of complex cells as a function of eccentricity was reported by Wilson and Sherman (1976). Payne and Berman (1983) found that at all eccentricities the tuning width of simple cells was smaller than complex cells but no systematic change in tuning width for either group was apparent. Kennedy and Orban's study (1979) supported Wilson and Sherman's results.

Gilbert (1977) observed a similarity in tuning for standard complex cells and simple cells with differences between complex and simple cells being most noticeable when infragranular layer complex cells were compared with the simple cell group. Simple cells were similar in tuning for all laminae. Leventhal and Hirsch (1978) reported data in agreement with Gilbert's observations.

The possibility has been raised of an anisotropy in the proportion of cells representing the vertical and horizontal meridians compared with oblique orientations (Rose and Blakemore, 1974). It has been further suggested that the anisotropy is class-dependent with differences in tuning properties of simple and complex cells related to their orientation preference (Rose and Blakemore, 1974). Psychophysical experiments in man have suggested that the thresholds for detection of stimuli near the principal vertical and horizontal meridians are lower than for the oblique (Campbell and Kulikowski 1966; Andrews, 1967; Mitchell, Freeman and Westheimer, 1967; Campbell and Maffei, 1971). The oblique effect has been demonstrated behaviourally for the monkey (Boltz, Harwerth and Smith, 1979; Williams,

Boothe, Kiorpes and Teller, 1981) and for the cat (Orban and Vandenbusche, 1979).

Rose and Blakemore (1974) reported a correlation for the oblique effect; orientation selectivity of simple cells was found to be inversely related to the angular distance of the preferred orientation from the principal meridians. No such correlation was found for complex cells. Wilson and Sherman (1976) could not confirm this result. Gilbert (1977) reported that no lamina was selective for a given orientation nor did any lamina have cells that were more sharply tuned than those in another lamina as would be anticipated from laminar differences in simple and complex cell distributions.

A possible substrate for the oblique effect might be an over-representation of neurones tuned to the horizontal and vertical. This has little support. Kelia and Whitteridge's (1973) claim that more than half of neurones in the cat's monocular segment of striate cortex prefer horizontally oriented stimuli was not supported in Wilson and Sherman's (1976) investigation. Similarly, Rose and Blakemore (1974) in cat, and Finlay, Schiller and Volman (1976) and Poggio, Doty and Talbot (1977) in monkey, found no differences in the number of cells tuned to the horizontal/vertical versus oblique. Mansfield (1974) and Mansfield and Ronner (1978) provided evidence that, for the macaque, cells tuned to horizontal and vertical are more numerous than those tuned to oblique orientations in the foveal projection region, but that various optimal orientations are seen in equal numbers in the parafoveal region. The conclusion was not supported in the

studies of Finlay, Schiller and Volman, (1976) and Poggio, Doty and Talbot (1977). DeValois, Yund and Hepler (1982) compared tuning of foveal and parafoveal simple and complex cells and concluded that, for the macaque, tuning width between the four groups was not significantly different. However, they reported that their foveal, but not parafoveal sample showed a meridional anisotropy with more cells tuned to horizontal/vertical. The statistical significance of the result was low (Chi-squared, P=0.07) thereby weakening their conclusion. In summary, there is no evidence that simple and complex cells differ in tuning properties as a function of meridional anisotropy.

Asymmetries in the tuning curve of simple and complex cells for moving contrast bars are evident in several studies (Rose and Blakemore, 1974; Henry, Dreher. and Bishop, 1974; Schiller, Finlay and Volman, 1976b; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978) though quantitative analysis was made in only two studies (Henry, Dreher and Bishop, 1974; Hammond and Andrews, 1978b). Henry, Dreher and Bishop introduced the measure of the ratio of the greater to the lesser half-width at half-height of the tuning curve as an index of symmetry. For a sample of forty simple cells, combining data for both light and dark bars for some cells, the mean asymmetry was 1.26 (range 1-2). The corresponding figure for complex cells was 1.62 (range 1-2.8). Hammond and Andrews (1978b) reported 60% of cells recorded in area 17 and 18 to be asymmetrically tuned in excess of 20% with ratios of half-widths ranging from 1.0-3.0, exceptionally 5.8. These authors found asymmetries to be more marked in area 18, than

17, except that area 18 hyper-complex type 2 cells (complex cells with end-inhibition), as a group, were relatively symmetrically tuned for orientation.

3.3 Dissociation of the Parameters of Orientation and Direction with Contrast Stimuli

Henry, Bishop and Dreher (1974) drew attention to the fact that the preferred direction of motion for a contrast bar is _necessarily_ orthogonal to the preferred orientation. Many studies have used moving bars for determining _orientation_ tuning. In such studies, the contributions of orientation and direction could not be assessed. These contributions have been assessed with contrast stimuli by making comparisons of tuning for moving and stationary bars (Henry, Dreher and Bishop, 1974), moving spots and bars (Henry, Dreher and Bishop, 1974) or by varying stimulus length symmetrically (Bodis-Wollner, Pollen and Ronner, 1976) or non-symmetrically (Rose, 1977; Hammond and Andrews, 1978 a, c) over the geometric centre of the receptive field. Those studies varying length symmetrically across the receptive field centre have assumed linearity of summation.

Henry, Bishop and Dreher (1974) compared tuning for stationary and moving bars, the stationary bar being aligned with the midpoint of the discharge centre. It was concluded that simple cells show identical tuning for a stationary bar and the same bar in motion. No detailed quantitative evaluation was made. Rose, in his doctoral thesis (Rose, 1978, p.28) noted from his data and from those of Blakemore

and Tobin (1972) that almost identical curves were obtained in
some cases but, in others, breadth of tuning differed by 50%.
Hammond and Andrews (1978, and unpublished observations)
observed tuning of some striate cortex neurones to be more
sharply and symmetrically tuned for a stationary bar than a
moving bar. There has been no quantitative comparison of
tuning for stationary and moving bars for complex cells.

Henry, Bishop and Dreher (1974) evaluated tuning for a
bar and spot moving through the geometric centre of the
receptive field. As in the evaluation for stationary and
moving bars no systematic quantitative consideration of data
was undertaken. For the unit illustrated, the preferred
direction (or axis in Henry et al's terminology) was
orthogonal to the cell's preferred orientation. For one
hypercomplex I cell (simple with end-inhibition) comparisons
were made for a spot with both a moving and stationary bar.
In each case, reduction in stimulus length brought about no
change in preferred direction but decreased response and
broadening of tuning; preferred direction therefore appeared
to be predictable from the response to a stationary flashed
bar.

From responses to moving spot and bar stimuli, Henry,
Bishop and Dreher (1974) identified two classes of complex
cells. For the first category, as for the simple cell,
decrease in bar length produced a reduced response with
broadening of tuning but no change in the cell's preferred
direction. For the second category, reducing stimulus length
similarly produced no change in preferred direction, a smaller

change in response <u>but</u> no change in tuning width. The existence of the second type of complex cell is doubtful. The tuning curves were derived from a limited range of directions and extension of the range could have revealed differences in breadth of tuning for the two stimuli. Summatory behaviour of the neurones would identify the group as the "special" complex category of Gilbert's (1977) classification, of which the cortico-tectal neurones of Palmer and Rosenquist's (1974) study are members. For a cortico-tectal neurone illustrated by Palmer and Rosenquist (1974), a broadening of tuning is apparent in the tuning curve for a spot compared with that for a bar.

Length-response curves for a bar moving at the cell's preferred orientation and moving in its preferred direction have indicated non-linearities of summation (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977). Bodis-Wollner, Pollen and Ronner (1976), though finding a general tendency for the length-response function to be linear over a considerable range, and in some cases the complete range, reported that, for most cells, non-linearities were evident before the optimal length was reached. Three factors contributed to the non-linearity.

(1) receptive field shape; some cells were found to have round or ovoid receptive fields and the summation of responses from excitatory zones of varying optimal lengths was seen to result in a non-linear length response curve.

(2) the central regions could contribute more to cell response than the lateral regions.

(3) a non-linearity arising from saturation of response at the

upper range of slit lengths.

In Rose's study (1977), cells were classified into three types according to the effects on the cells' responses of extending bar length beyond the central region of the receptive field. The cells were further divided into three groups depending on their responsiveness to very short bars crossing the receptive field centre. By the first classificatory system, cells were divided into facilitatory flanks (FF), no flanks (NF) and inhibitory flanks (IF). On the basis of their spot responses, cells were grouped into US (unresponsive), PS (cells whose length-response is linear up to a limit) and RS (cells responding very well to small spots). A cell would therefore be placed in one of nine groups. No significant differences in the distributions of the nine groups between simple and complex cells was found. The functional properties of the nine groups could be summarized as follows:

(1) cells with inhibitory flanks respond well to spots whereas cells with facilitatory flanks require summation within the field centre before they fire;

(2) the more responsive a cell is to spots, the shorter is its receptive field centre, with centre length increasing with distance of the field from the area centralis;

(3) field size is positively correlated with field centre size, both for FF and IF cells. Type FF cells have stronger flanks than IF cells. The stronger the flanks of type IF cells the shorter the flanks are and cells responsive to spots also have short flanks.

(4) length response behaviour is related to orientation

selectivity; cells with strong facilitatory flanks tend to be narrowly tuned for orientation while cells with strong inhibitory flanks respond over a wide range of orientations.

Rose used the conditions to establish how the component parts of the receptive field interact. In the first condition, a short bar was moved through the receptive field but its axis of movement was displaced laterally after eight to ten presentations to stimulate different parallel strips of the receptive field. A second condition used a very short bar with one end always moving along the line bisecting the minimum response field which after 8-10 presentations, was extended by a small amount at its peripheral end only; one half of the receptive field was not stimulated at all and the other half was stimulated more and more from the centre outwards. For the third condition, an initially short bar passing well to one side of the field centre, was extended gradually to form a very long bar crossing the whole receptive field. For each condition the bar was presented at the optimal orientation and the total number of spikes as the bar traversed the field was counted.

No obvious asymmetries in the strengths or the sizes of the flanks on each side were apparent (c.f. Hammond and Andrews, 1978b). Although the initial segment of the length response tuning curve often rose linearly up to the boundary of the receptive field centre, summation was strictly linear only if the cell was type PS. For type RS cells, the responses to a stimulus covering the whole central region were less, and for the type US cells greater, than the sum of

responses to shorter bars. Summation of the centre and flank components must also be non-linear because facilitatory flanks do not (by definition) drive the cell when stimulated alone nor do inhibiting flanks suppress firing when they are stimulated in isolation.

Hammond and Andrews, in a series of papers (Hammond and Andrews, 1978a, b, c) produced an extensive study of the effect of stimulus length on response magnitude and tuning. Though their data were drawn from recordings in area 18, their results provide interesting observations on how the component parts of a receptive field may interact. The extent to which these authors' observations are specific to that area or whether the properties reported are descriptive of simple and/or complex cells of striate cortex requires a replication of their experiments in area 17. With these considerations in mind, their studies are described with an emphasis on the possibilities they raise for complexities of receptive field organization.

Hammond and Andrews (1978c) found that, for area 18 cells, interaction within receptive field halves could be facilitatory, additive, partially additive, or subtractive and that the organization within one half was not predictable from that in the other. Moreover, interactions between halves could be facilitatory, additive, partially additive, or subtractive and could not be predicted from interaction within halves. Hammond and Andrews argued for a (minimal) division of the receptive field into halves, with summation between halves differing from that within each half-field.

Hammond and Andrews (1978a) considered the half-field in terms of its orientation tuning properties. Some area 18 cells were found to have dissimilar preferred orientations for each receptive field half. In cells whose receptive field halves were similarly tuned, broadly tuned, or apparently untuned for orientation, simultaneous stimulation of both halves of the receptive field led to substantial sharpening of tuning.

Collating the data from length-response, orientation and symmetry of tuning studies, Hammond and Andrews (1978c) observed that the zones which make up the receptive field interact in a complex way. To produce the length summation data it is necessary to involve summation of signals _within_ each half field (partial, complete, or subtractive if inhibition is present, and with differences between each half-field) and, secondly, there is an interaction _between_ the two half-field signals (summative, partially summative, facilitatory or inhibitory). To account for the orientation tuning results, a third summative principle would be required and it was suggested that different inhibitory bands facilitate one another, the degree of facilitation varying between cells. In addition, Hammond and Andrews commented that the zones of the half-fields must differ in some way, causing asymmetrical tuning and dissimilar tuning for the two halves, though they pointed out these differences may be of geometry rather of summative principle.

3.4 The Tuning of Complex Cells for Contrast and Textured Stimuli

For the majority of complex cells, the preferred directions for moving contrast bars and fields of visual noise are different (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980a, b). Hammond (1978) found that the majority (fifty-two) of his sample of sixty-two neurones showed significant differences in preferred directions for bar and noise. The average difference in tuning peaks for bar and texture reported by Hammond (1978) was 30-40 deg. Greater peak separation was reported for complex cells of the infragranular layers (Hammond and MacKay, 1977; Hammond, 1978), that is those more responsive to visual noise (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980a, b). Tuning for bars was found to be sharper than for noise, as would be expected, since orientation tuning is well known to depend on contour length (Henry, Bishop and Dreher, 1974; Gilbert, 1977; Hammond and Andrews, 1978b). For cells asymmetrically tuned for bar stimuli, tuning has been reported to be broader on the flank of the tuning curve closest to the preferred direction for noise (Hammond, 1978).

According to Hammond (1978), compared with a moving bar stimulus, moving noise fields enhance complex cell directional bias; cells directionally biased for a bar may be directionally selective for noise. Two thirds of a sample of forty-nine neurones directionally biased for bars were directionally selective for noise, ten of these showing suppression of firing to noise moving in the null direction.

A further twenty-three cells were directionally selective for bar stimuli _and_ noise, nine with suppression of firing in the null direction.

The tuning curve for texture takes two forms;   a single peak in the tuning curve (unimodal cells) or a bimodal tuning with depression of response around the peak in the bar tuning curve (bimodal cells) (Hammond, 1978; Hammond and Reck, 1980a, b). Peaks of the noise tuning curve for bimodal cells may be symmetrically or asymmetrically located about the peak for bar tuning (Hammond, 1978). Preferred velocity and velocity bandpass are invariably higher for texture motion than bar motion.   Texture tuning profiles are typically unimodal at low velocities and increasingly bimodal at higher velocities (Hammond and Reck, 1980a, b), whereas bar tuning is essentially velocity invariant (Hammond, 1978; Hammond and Reck, 1980b).

3.5 Tuning for Contrast and Textured Stimuli and Models

In response to moving contrast bars, the tuning curve of simple cells is generally sharper than that of complex cells. The length-response function is essentially non-linear, reflecting complex interactions within and between half-fields. The assumptions of Bishop's group (Bishop, Coombs and Henry 1971b; Goodwin and Henry, 1975) and Schiller, Finlay and Volman (1976b, e), that a bar is a linear sum of component spots is unsupported (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977; Hammond and Andrews, 1978c).

Tuning shown by simple cells for stationary and moving bars is identical. Moreover, the preferred direction for a moving spot is orthogonal to the cell's preferred orientation. These findings are in accord with Bishop's model. Since, however, the data were based on cells showing symmetrical tuning for moving bars the support given by the data to the model is limited. Asymmetrically tuned units are problematical for Bishop's model. Given the primary role of the inhibitory sidebands in determining orientation tuning (Henry and Bishop, 1972; Henry, Dreher and Bishop, 1974), asymmetrical tuning would reflect the asymmetric location of one sideband in relation to the central discharge zone. The principle of a fixed spatial relationship between intracortical inhibition and afferent excitation would therefore be denied. It has previously been argued both that inhibition outside the discharge zone has no separate role in orientation tuning and that intracortical inhibition has no fixed spatial relationship to the afferent input.

It was suggested that the tuning properties of simple cells might be accounted for by reference to the model of Goodwin, Henry and Bishop (1975) for direction selectivity. This would also predict that tuning for moving and stationary bars would be identical. For a cell asymmetrically tuned for a moving bar, this would imply that the spatial organization of the receptive field, determined when the sensitivity profile is mapped with a stationary flashed bar, would show an asymmetry. Preferred direction for a spot would also be predictable from the response to a stationary edge. The data from Henry, Bishop and Dreher's study (1974) and Goodwin and

Henry's (1975) paper are inadequate to test these predictions.

Complications arise when the complex cell is considered.
The direction-selective response produced by a moving field of
noise demonstrates that the luminance increment caused by a
stationary edge is neither the sufficient nor the necessary
condition for a direction selective response for that cell
type. To date no study has been made of the parameters
contributing to direction-specific inhibition for contrast and
textured stimuli.

The origin of the bimodal tuning for moving noise fields
has provoked much discussion (Hammond, 1978; Hammond and
Reck, 1980b; Hammond and Smith, 1983). The possibility that
it is artefactual has been raised by Movshon (cited by Hammond
and Smith, 1983), who suggests that the bimodality represents
the response to the vector of velocity in the cell's preferred
direction. Several arguments weigh against this possibility.
Some cells remain unimodal at velocities of motion beyond the
high velocity cut-off point for an oriented stimulus (Hammond
and Smith, 1983) and other cells are bimodal at velocities
beyond that producing response to a moving bar and at
velocities below that optimal for texture (Hammond and Smith,
1983). The two lobes for texture tuning at higher velocities
of motion are often asymmetrical and differ in width and
strength (Hammond, 1978; Hammond and Reck, 1980b; Hammond
and Smith, 1983). The trough in the texture field tuning
curve corresponds to the bar tuning peak, but can persist at
velocities beyond the cut-off point for producing a bar
response (Hammond and Smith, 1983). Depression of texture

sensitivity is greatest at high velocities when response is driven below the cell's resting discharge level (Hammond and Reck, 1980b).

Hammond (Hammond, 1978; Hammond and Reck, 1980b; Hammond and Smith, 1983) sought to explain the bimodality in the texture field tuning curve as a product of the directional mechanism alone or from an interaction between orientation and direction mechanisms. Two possibilities for the direction mechanism alone were suggested; that the depression of response might arise as a result of self-inhibitory feedback preventing cell overload, or through inhibitory convergence from neighbouring cells. In the latter case, inhibitory input from cells in the same or different laminae, with similar preferred directions would cause depression of response. Excitation would be maximal for directions to either side of that preferred by the cell. The suggestion is similar to that proposed by Sillito (1979) for the orientation domain with inhibitory contributions to orientation selectivity being greatest not at the preferred orientation but to either side of the preferred orientation.

Hammond (1978) has noted that it would be difficult to account for the depressed sensitivity in texture tuning of bimodally-tuned cells in the vicinity of the peak in bar tuning without invoking some interaction between direction and orientation mechanisms. There is direct evidence of such an interaction. Hammond (1981a) and Hammond and Smith (1983) reported the response of complex cells to in-phase motion of bar and texture over a range of velocities of stimulus

movement. At higher velocities the directional tuning profile
for bar and texture was found to be comparable to the addition
of the direction tuning profiles for each stimulus alone.   As
stimulus velocity was reduced, however, the tuning profile for
simultaneous motion of bar and texture   was   found   to
increasingly   resemble   that   for   the   bar   alone.   The
interpretation was that a cell's responsiveness to texture
backgrounds is vetoed by a simultaneous signal arriving at its
bar-sensitive input. A problem for the interpretation that
depression of texture tuning reflects an interaction between
orientation and direction mechanisms is that, as   reported   by
Hammond and Reck (1980b), the trough may be more pronounced
above the optimal velocity for bar and broader than the total
width of the bar tuning curve.

To date, little quantitative data have been available to
assess the contributions of orientation and direction to the
tuning properties. of complex cells for contrast stimuli.
Furthermore, complexities indicated by studies of tuning for
textured stimuli suggest differences of receptive   field
structure which cannot be accounted for by models developed to
explain the simple cell's response to contrast stimuli.   A
combination of contrast and textured stimuli has therefore
been used to assess the tuning properties and receptive field
structure of complex cells in cat striate cortex.

CHAPTER FOUR: THE CONTRIBUTION OF ORIENTATION AND DIRECTION
TO THE TUNING PROPERTIES OF COMPLEX CELLS

Introduction

Orientation selectivity has classically been assessed
with moving contrast bars (Hubel and Wiesel, 1962, 1963;
Henry, Dreher and Bishop, 1974) and orientation has not been
dissociated from direction. For a moving bar, direction is
necessarily orthogonal to orientation (Henry, Bishop and
Dreher, 1974). Comparisons of tuning for bars and moving
fields of visual noise indicate the mediation of orientation
and direction by separate mechanisms (Hammond, 1978 and
subsequently). Though some consideration has been given to
the contributions of orientation and direction to the simple
cell's response, using contrast stimuli (Henry, Bishop and
Dreher, 1974), corresponding data for the complex cell are
scant. Moving fields of visual noise overcome the summatory
requirements for effective drive of many cortical neurones and
at the same time provide a stimulus free from inherent
orientation. A combination of contrast and textured stimuli
have therefore been used to assess the contributions of
orientation and direction to the complex cell's response.

It is of interest, not only from the perspective of
receptive field organization, but also for an understanding of
their functional role in visual analysis, to investigate
complex cells' tuning properties. In Hubel and Wiesel's
model, the single cell was given a role in contour analysis in
a hierarchical process of feature extraction. Representation

of form at the level of the single cell has been questioned (see chapter 5 for discussion). To fulfil a universal role in contour analysis cortical cells should respond selectively not only to contours of luminance but also, for example, contours of colour or texture. Discontinuities of texture density, as Hammond and MacKay (1977) have pointed out, even without any change in mean luminance, can outline a contour as unmistakably as those of colour or luminance. Even with uniform texture, discontinuities of texture velocity, such as "texture contours" produced when a camouflaged animal moves against a stationary background, can reveal the outline of an otherwise undetectable object. The stimulus provided by a bar of texture moving across a field of similar texture and equal mean luminance is of interest in this context since, though camouflaged when at rest, in motion both its form and motion are perceived. A comparison of tuning for this stimulus with stimuli in which the attributes of either form or motion are present would contribute to the understanding of the role of the single cell in perception.

Consideration was therefore given to the tuning properties of complex cells to contrast and textured stimuli in which the parameters of orientation and direction were dissociated. Three specific objectives were set.

(1) To evaluate tuning for a stationary flashed contrast bar and the same bar in motion.

(2) To compare these results with tuning for a spot moving through the geometric centre of the receptive field and tuning for a moving field of visual noise, to assess the contributions from orientation and direction selective

mechanisms.

(3) To evaluate tuning for a texture bar moving across a field
of visual noise of similar texture and equal mean luminance,
to determine whether tuning is biased towards tuning for a
contrast bar or whether, in the absence of luminance cues,
cells are sensitive only to texture bar <u>motion</u>.

4.1 Animal Preparation

The semi-chronic preparation (Hammond, 1979) was used for
the experiments. Attached to the skull were a stainless-steel
peg and a perspex chamber, the former providing an atraumatic
head restraint during recording sessions and the latter a
means of access to the visual cortex. Figure 4.1 shows the
semi-chronic preparation used for the experiments (after
Hammond, 1979). To ensure accurate stereotaxis, an
individually adjusted bridge retained the animal's head in
standard stereotaxic co-ordinates by anchoring the peg. The
perspex chamber was centred over the sagittal suture with
anterior/posterior co-ordinates for the mid-point of the
chamber close to P5. The chamber was marked during
implantation with four grooves, the stereotaxic co-ordinates
of which were established in order to provide reference points
for the location of electrodes during recording sessions.

Implantation of peg and chamber was carried out under
surgical anaesthesia provided by a mixture of 2% halothane
with 72.5% nitrous oxide : 27.5% oxygen. A midline incision
of the scalp was made and, following disinsertion and
retraction of the temporalis muscles, the chamber and peg were

A Semi-chronic Preparation for Cortical Recording

The figure illustrates the preparation used for recordings from
the striate cortex. Attached to the skull are a stainless-steel
peg and a perspex chamber. By means of the peg, in conjunction
with an individually adjusted bridge, the animal's head is held
atraumatically with accurate stereotaxis. The perspex chamber
provides access to the striate cortex and additionally serves to
provide reference points for stereotaxic location of electrodes.
(Reference points are grooves on the top of the chamber). Fixed
in the wall of the chamber are sockets for terminals for
connection of leads for monitoring the EEG. The insert shows the
location of the peg and chamber.

PERSPEX RECORDING CHAMBER

Dimensions in mm.

TOP VIEW

ANTERIOR

BOTTOM VIEW

LATERAL VIEW

Teflon-insulated EEG leads from gold-plated terminals.
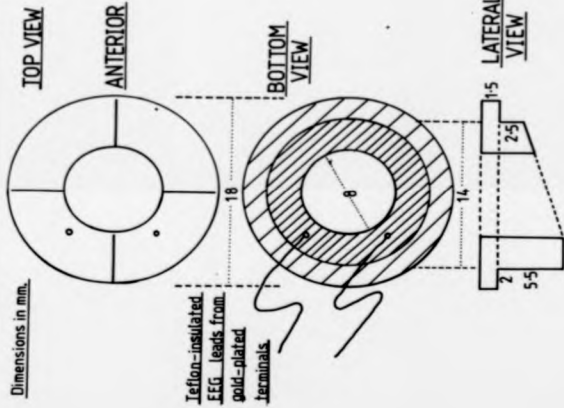
ANTERIOR VIEW

LATERAL VIEW
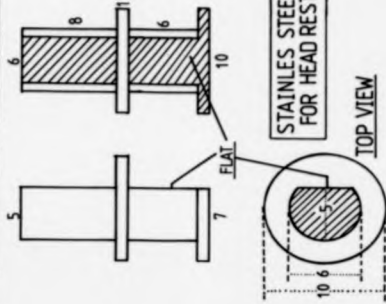
STAINLES STEEL PEG FOR HEAD RESTRAINT

TOP VIEW

FLAT

LOCATION OF CHAMBER & PEG

PEG

ACRYLIC

CHAMBER
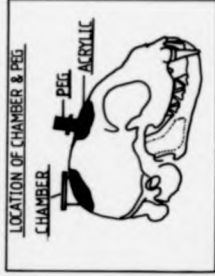
fixed to the skull with dental acrylic and anchored to the skull by means of six stainless steel screws. Two of these screws additionally functioned as terminals for EEG monitoring; one located over the primary auditory cortex and the other over extra-striate visual cortex. Teflon-insulated wires lead from these terminals to gold-plated pins, fixed in the chamber wall, to which wires were connected during recording sessions for EEG monitoring. Following implantation, the scalp was sutured around the implant with Michel clips and the wound margins protected by overlapping flanges on the peg and chamber. Topical application of Xylocaine spray (Astra) provided local anaesthesia of the wound during the recovery period and localised application of Cicatrin powder (Wellcome), together with intramuscular procaine penicillin (30 mg/kg), before and after implantation, and during the recovery period, ensured infection-free recovery. Suture clips were removed 10-14 days after implantation.

4.2 Recording Sessions

Animals were used for recording sessions of approximately nine hours including preparation and reversal periods. A minimum space of two clear days between recording sessions was standard practice, with an individual animal being used no more than three times in any two week period. Anaesthesia was induced with a mixture of halothane (Fluothane, ICI) initially 3% rising to 5%, with 72.5% nitrous oxide: 27.5% oxygen. Single-cell recordings were made under light anaesthesia maintained with the same composition of nitrous oxide/ oxygen

supplemented with 0.3-0.7% halothane. Ventilation was via a McGill cuffed endotracheal tube (3.0-4.5mm) inserted after coating with the local anaesthetic gel Xylocaine (Astra). Ventilation rate and stroke volume were under the control of a Palmer ("Ideal") pump. Ventilation rate was set at 28 strokes/min. The stroke volume was adjusted to maintain an end-tidal carbon dioxide percentage of between 3.8-4.0% End-tidal carbon dioxide was monitored, breath by breath, by an infrared medical gas analyser (Beckman, LB2) and registered for the duration of the experiments on a Washington 400 MD/2 pen recorder.

Care was taken with this lightly anaesthetized preparation to maintain an adequate level of anaesthesia by constant reference to the various indices of anaesthetic level, principally the EEG but additionally the ECG, pulse rate, end-tidal carbon dioxide, temperature, and firing rate of recorded units. The EEG was constantly monitored and an adequate depth of anaesthesia ensured by reference to the presence of spindles in the EEG and amplitude of the EEG. Heart rate was observed to maintain a norm of three beats per second. Permanent records were kept of the carbon dioxide levels, EEG, heart rate and spike firing rates. The temperature of the animal was maintained by a homoeothermic blanket control (type 8185, CF Palmer) with body temperature monitored by a rectal thermistor introduced with a lubricant gel. Body temperature was maintained at 38.75 deg. centigrade.

Eye preparation and paralysis were conventional.

Phenylephrine hydrochloride (10%) and atropine methanitrite (1%) (Minims, Smith and Nephew) were used to retract the lids and nictitating membranes and to dilate the pupils. The corneae were protected with neutral contact lenses (two-curve lenses, Hamblin). The contact lenses were applied with sulphacetamide (10%) (Minims, Smith and Nephew Ltd.) and the wetting agent Transol (Smith and Nephew, Ltd.) was applied to the exposed surfaces of the eyes not covered by the lenses. The lenses had base/peripheral curves of either 8.0/8.5 or 8.5/9.0 mm., both with base/peripheral diameter 8.0/12.0 mm. according to the relation:-

$$Y = 7.28 + 0.34X$$

derived by Andrews and Hammond (1970), relating the corneal radius of curvature (Y mm) and body weight (X kg), and based on the data of Bishop, Kozak and Vakkur (1962) and Vakkur, Bishop and Kozak (1969). Artificial pupils, 5mm. in diameter, were mounted in front of the contact lenses by flexible frames attached to the bridge.

The refractive correction required to focus the eyes at a distance of 57 cm. on the screen of a Hewlett-Packard display, on which stimuli were presented, was determined by slit-retinoscopy. At that distance, one centimetre on the screen was equivalent to one degree of visual angle. Supplementary lenses (range -3.0 to +4.5 dioptres) in steps of 0.25 dioptres were used to provide the appropriate optical correction where required. Using the back projection method of Fernald and Chase (1971), the position of the area

centralis of each eye was marked on a perspex screen in front of the Hewlett-Packard display unit. Receptive field positions were located with reference to these positions. Paralysis of the eyes was achieved by an initial dose of 0.5ml gallamine triethiodide (Flaxedil, May and Baker, 40 mg/ml) with a subsequent infusion of 7-10 mg/kg/hr via a Butterfly cannula (23G or 25G, Abbott) inserted in the left cephalic vein.

A standard procedure for recovery from paralysis and anaesthesia was followed. Infusion of Flaxedil was terminated approximately one and a half hours before the end of the recording session and excess remaining in the cannula was flushed through with sterile saline. On completion of the recording session, procaine penicillin (30 mg/kg) was administered intramuscularly. Atropine sulphate (0.1 ml at 0.06 mg/ml), to prevent spasm, and neostigmine methylsulphate (typically 0.2 mg. at 0.5 mg/ml) to antagonize any residual non-metabolised Flaxedil were given via the cannula. The exact amount of neostigmine administered was titrated against the animal's recovery of spontaneous breathing which was frequently tested during the recovery period. The craniotomy was cleaned, treated with Cicatrin powder and capped. After removal of the contact lenses, the eyes were irrigated with sulphacetamide (10%) (Minims, Smith and Nephew Ltd) and wetting agent (Transol, Smith and Nephew) was applied.

4.3 Equipment for the Generation of Visual Stimuli

The apparatus described in MacKay and Yates (1975) and Hammond and MacKay (1977) was used to generate visual stimuli. A square raster of 256 lines, each of 256 elements was modulated by a special purpose generator using digital integrated circuits to present up to 50 picture frames per second. Two independent 16-stage fed back shift registers made available two pseudorandom pulse trains NA and NB each of which could be reset and locked in phase from one frame to the next so as to give a static noise texture. The noise field subtended a ten by ten degree square. The phases of NA and NB could also be manually adjusted to control against the possibility that accidental features of a particular noise field might be responsible for specific response peaks. Grain sizes of the noise fields averaged 4 min of arc. An electronic changeover switch, driven by a gating circuit, defined a moveable rectangular window of the raster which could be painted by NA, NB or a steady black or white signal at will. Where contrast stimuli formed the window - spots or bars of various dimensions - relative luminance levels were set at 0.6 log units below noise background (black bar) or 0.25 log units above the noise background (white). Mid-mesopic levels of illumination were used with average screen luminance of around 0.9 log cd/m sq. in conjunction with 5mm diameter artificial pupils (Ahmed, Hammond and Nothdurft, 1977). A conventional sine-cosine potentiometer circuit (MacKay and Fisher, 1962) allowed calibrated rotation of the XY plane. Contrast stimuli could be moved relative to a stationary background of static noise or flashed with the

noise as background, the contrast bar replacing the noise field in that rectangle. Alternatively, a noise bar could be moved relative to the noise background or the noise field could be moved in isolation.

4.4 Cell Recordings

Extracellular recordings were made with glass pipettes filled with 4M sodium chloride with tip sizes averaging 2 microns with impedance values of between 0.65 and 1.3 Meg Ohms at calibration and up to 2 Meg Ohms in the cortex. Electrodes were introduced into the cortex via a dural puncture made with a sterile syringe needle (no. 12; 0.7 x 32mm) fixed by an adaptor to a microdrive mounted on a micro-manipulator. Stereotaxic positioning of the electrode was achieved by reference to the marks made on the chamber as previously described. Electrodes were located at stereotaxic co-ordinates between 1.5 and 1.7mm of the midline and between 4.0 and 6.0 mm behind the interaural plane. On insertion of the electrode, the cortex was stabilized by sealing in the electrode with warm 2% sterile agar in 0.9% saline, filling the chamber with solution. Cell search was accomplished by fine vertical movements under the control of an hydraulic microdrive.

4.5 Recording Equipment

Spike amplification and discrimination were conventional with raw spikes displayed on a dual-beam oscilloscope (Tektronix RM 565) and monitored by an audio-monitor.

Stimulus direction

90°+270°
170°+350°
180°+0°
260°+80°
Resting discharge

Texture motion

Bar motion

Stimulus sequence

Time [s]

Stimulus sweep
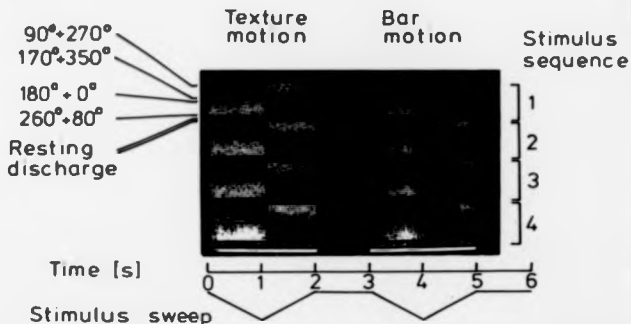
Fig 4.2

Dot display for registering spikes during recording of tuning curves (after Hammond 1981a, fig. 2).

The response to a forward and backward sweep of each pair of stimuli is represented by a single row of the display. Between each row, direction has been stepped by 10deg. Direction of motion is specified from 0 to 350 deg. measured clockwise from vertically upward motion. The complete display is made up from four round-the-clock sequences. Each of these sequences consists of data from eighteen pairs of directions; two blocks of nine followed by two complete cycles with only the stationary noise background present. The stimulus cycle at the foot of the diagram allows it to be related to fig. 4.3.

Discrimination was provided by a level and window
discriminator. Discriminated spikes were displayed as:

(1) spike rate on a linearized pen recorder (Washington, 400
MD/2);

(2) a dot display on a single beam storage oscilloscope
(Tektronix, 5111) with each dot representing a discriminated
spike (see fig 4.2 and accompanying explanation);

(3) an averaged response histogram by means of a Biomac 1000
data retrieval computer (Data Labs);

(4) individual counts by electronic counters (Advance, TC 11A)
for gated periods of the stimulus cycle. The counters could
be reset between cycles or could be used to provide cumulative
counts.

Data were stored for off-line analysis on cassette tapes
used in conjunction with a Bell and Howell (CR 3000)
four-channel, AM/FM tape-recorder. Dot displays were stored
on polaroid photographs. Tuning curves, obtained by the
method of Hammond (1978) and Hammond and Reck (1980a, b),
described below, were produced on an analogue (Bryans, 29000)
XY plotter from the output of the Biomac in the four-channel
mode.

4.6 Determination of Direction and Orientation Tuning-Curves

A modified version of the multihistogram method of Henry,
Tupper and Dreher (1973) was used. The method was developed
by Hammond (Hammond, 1978, 1981a; Hammond and Reck 1980a, b).
The stimulus cycle was of six seconds duration and initiated
by a synchronization pulse. In the first two seconds the

field of texture moved in one direction followed by its opposite. During the third second of the cycle, the texture-field remained stationary and a stationary contrast bar was presented with the noise field as background. The bar replaced the noise as a moveable rectangular window and was defined by a changeover switch driven by a gating circuit. Alternation between the noise and bar was provided by a reed relay. During the fourth and fifth seconds the bar was moved in the directions previously traversed by the noise field. During the sixth second, the direction/orientation of the stimulus was stepped by ten degrees i.e. during the one second pause before the onset of texture-field motion. Direction was stepped clockwise.

For the generation of tuning curves for stationary, flashed contrast bars, the texture-field remained stationary for the complete six-second cycle. In the early experiments, a black or white bar was flashed for a period of one second during the fourth · second of the stimulus cycle. When stationary bars were presented under conditions of contrast reversal, a white bar was presented during the first to third seconds of the cycle. For the duration of the fourth second, contrast was reversed, the white bar becoming a black bar. For the fifth second, contrast was reversed again and a white bar presented.

A total of eighteen sweeps provided the data for tuning curves in paired comparisons between texture-field motion and a contrast stimulus or texture bar. Two additional cycles, during which only a stationary texture-field was presented,

provided a measure of the cell's resting discharge level. The sequence of eighteen sweeps was taken in two blocks of nine for reasons of convenience. Tuning curves were produced on an analogue XY plotter (Bryans, 29000) in conjunction with a Biomac 1000 (Data Labs). The discriminated pulses were fed into the Biomac for accumulation in sequential bins, in a single channel mode, during the first, second, fourth and fifth seconds. Bin advance was controlled externally by pulses arriving 1, 2, 4 and 5 seconds after the start of each cycle. Data for the first stimulus were thus entered into bins 1,5,9 ...77 (forward texture motion) and 2,6,10...78 (backward texture motion); those for the second stimulus into bins 3,7,11...79 (forward bar motion) and 4,8,12...80 (backward bar motion) respectively. Four round-the-clock sequences formed the total data collection cycle. Tuning curves were derived by outputting the single-channel stored data through four channels, each channel containing half a tuning curve for a particular stimulus. In addition to the sets of tuning curves with simultaneously recorded measures of resting discharge, a calibration signal (200 Hz) was added after the final round-the-clock sequence, providing a standard for evaluation of spike firing in the tuning curves (bins 81-88, i.e. 2 bins per channel, corresponding to an impulse firing rate of 50/sec. in the case of 4 complete sequences). The method is illustrated in fig 4.3.
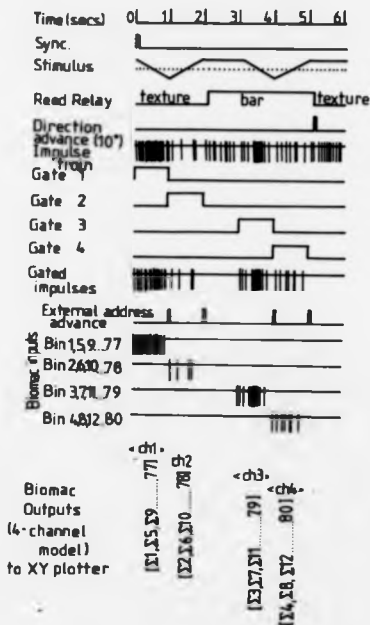
Fig 4.3

Illustrating data accumulation for determination of tuning curves (after Hammond, 1981a).

The stimulus cycle was initiated by a synchronization pulse.
Discriminated spikes were fed into the Biomac for accumulation
in sequential bins in a single channel mode. Data for texture
motion were entered into bins 1, 5, 9 ..77 (forward motion)
and 2, 6, 10 ..78 (backward motion) and those for the second
stimulus into bins 3, 7, 11 ..79 (forward motion) and 4, 8, 12
..80 (backward motion). Data were collected from four round-
the-clock sequences. Tuning curves were derived by outputting
the single-channel stored data through four channels, each
channel containing half a tuning curve for a particular stimulus.

4.7 Experimental Strategy

Cell search was carried out using combined presentation of bar and texture-field moving in phase. Cells were classified as complex by the absence of a division of the receptive field into discrete on and off areas (Hubel and Wiesel, 1962, 1963), into "Standard" and "Special" complex by the criteria of Gilbert (1977) and "Standard" complex cells were further classified as B cells by the criteria of Henry, Lund and Harvey (1978). Ocular dominance was assessed and the non-dominant eye occluded. Receptive fields were plotted as "minimum response fields" (Barlow, Blakemore and Pettigrew, 1967). Stimulus parameters were then optimized for the dominant eye. End-inhibition was tested by reference to the length-response curve; cells showing a significant reduction of response when length was increased beyond an optimal value were classified as showing end-inhibition. Quantitative descriptions are made for cells which did not exhibit end-inhibition so-defined. Three cells with end-inhibition were recorded for which qualitative observations are made.

Paired comparisons of tuning were made for the following stimulus combinations:
(1) moving field of visual noise versus moving contrast bar;
(2) moving field of visual noise versus moving contrast spot;
(3) moving field of visual noise versus moving texture bar;
(4) stationary noise field with black and white bars flashed.

Tuning for the moving spot was made with the spot moving through the geometric centre of the minimum response field.

In the stationary bar condition, the bar was rotated symmetrically about the geometric centre of the field and the moving bar was moved symmetrically through the receptive field, taking the geometric centre as reference point. Tuning curves were obtained in pairs with the stimuli being interleaved during recording of responses for each direction of motion in round-the-clock sequences. One member of the pair, a moving texture-field, remained constant. Keeping one member of the pair of stimuli constant, when a complete range of stimuli was used, allowed any time-dependent changes in responsiveness to be monitored. In order to prevent differences in responsiveness during the course of the experiment biasing results, stimulus order was randomized and repeated measures were made from time to time during the course of experiments. The texture sample was routinely changed and for evaluation of tuning for .texture bars, tuning curves for each cell were obtained for two samples of visual noise.

4.8 RESULTS

Data were obtained from eighty well-discriminated units from a total of 9 cats. Of these, three units showed end-inhibition and are not included in the quantitative description of data. The remaining seventy-seven units included twenty-six standard complex and twenty special complex cells; thirteen standard complex cells showing a single peak for texture field tuning (unimodal standard cells) and thirteen standard complex cells showing a double peak for texture tuning (bimodal standard complex cells), thirteen

unimodal special complex cells and seven bimodal special complex cells. One B cell was recorded and found to show tuning properties identical to other standard complex cells with which it is included. An additional thirty-one complex cells, not classified into standard and special complex cells, provided data for some of the stimulus conditions; moving contrast bar or spot, moving texture-bar or stationary bar. Twenty-nine of these units were unimodal and two bimodal in their texture-field response. All units had receptive fields within ten degrees of the area centralis.

The original observations of Hammond and MacKay, (1977), Hammond, (1978) and Hammond and Reck, (1980a, b) were confirmed. Only complex cells showed a response to moving texture fields and texture bars; seven simple cells tested with these stimuli showed no significant response. The texture field response was velocity-dependent and took unimodal or bimodal forms. Ocular dominance differences between bar and texture were frequently observed, though ocular dominance differences were not pursued in the present study. Comparison of tuning for bar and texture fields in motion revealed differences in peak position for the two stimuli with depression of texture sensitivity associated with the peak in bar tuning. For units showing a unimodal texture-field response, mean peak separation was found to be 32.9 degrees. By reference to lamina IV small field, monocular simple cells, the distribution of complex cells between the supragranular and infragranular layers was assessed. Of the 77 cells, 21 (27%) were located in the supragranular layers and 56 (73%) in the infragranular layers.

4.8(a) Comparison of Tuning for Moving and Stationary Bars

Measurements were made of peak, tuning width and symmetry
of tuning for moving and stationary bars and determined with
linear regression lines fitted to the two flanks of the tuning
curve. The peak was defined by the intersection of the
regression lines, and breadth of tuning by the full and
half-width at half height, allowing for resting discharge.
Symmetry was defined by the ratio of the greater to the lesser
half-width.

Following the convention of Hammond (1978), the term
direction replaces the term axis used in Henry, Dreher and
Bishop's (1974) study. Direction sensitivity is a vector of
response magnitude in any specified direction between 0 deg to
360 deg (measured clockwise from vertically upward motion and,
for convenience, a bar stimulus is specified by its direction
of motion, orientation orthogonal to direction, rather than
its orientation per.se). For easy comparison of tuning for a
stationary with a moving contrast bar, stationary bars are
defined with reference to the direction taken for the same bar
in motion. For example, a vertically oriented bar has the
value 90 deg, corresponding to the direction in which bar
movement would take place.

Data for assessment of symmetry of tuning were available
for a total of 77 units. Fifty-five were unimodally tuned for
texture of which the majority were asymmetrically tuned for
bar motion, the wider flank adjacent to the tuning curve for
texture field motion (c.f. Hammond, 1978). One unit,

unimodal in texture-field tuning, had the broader flank not adjacent to the texture-field tuning curve and, to maintain overall consistency in the presentation of data, this unit's symmetry of tuning is defined by the ratio of the half-widths with the flank adjacent to the texture-field as the numerator. This unit (176/2) therefore is identified by a symmetry ratio of less than one (0.9). This unit was unresponsive to a flashed bar. Excluding this unit, asymmetry ranged from 1.1 to 2.5, exceptionally 3.2 with a mean value of 1.8 (data summary table 1). Units bimodally-tuned for texture (twenty-two) were either symmetrically or asymmetrically tuned for moving bar, as Hammond (1978) has also reported. Those units _asymmetrically_ tuned for bar motion were characterized by one peak of the texture tuning curve being more prominent. Conversely, cells _symmetrically_ tuned had texture-field tuning with the two peaks equally prominent. The values for symmetry of tuning for the bimodal cells ranged from 1.0 to 1.6, exceptionally 2.6 with a mean of 1.3 (data summary table 2).

4.8(b) Tuning for Moving Contrast Bars as a Function of Deviation of a Cell's Preferred Orientation from the Principal Meridians

In order to assess whether, in the population of cells sampled, there was a non-uniformity in the proportion of complex cells representing horizontal/vertical or oblique orientations and whether tuning for a moving bar is related to the deviation of a cell's preferred orientation from the principal meridians, breadth and symmetry of tuning as a function of preferred orientation was evaluated. In figure

4.4, the distribution of preferred orientations, as a function
of deviation from the principal meridians, for the population
of seventy-seven cells, is shown. Whilst there is not an
exact equivalence in numbers of cells representing each range
of orientations, there is no evidence from the histogram of an
overrepresentation of cells tuned to the principal meridians
or oblique orientations.

In figures 4.5 and 4.6, breadth and symmetry of tuning
for a moving bar are plotted as a function of deviation of a
cell's preferred orientation from the principal meridians. As
can be seen from fig. 4.5, there is a wide scatter in breadth
of tuning for most orientations. Though the two most
broadly-tuned units have preferred orientations which are
oblique, and cells with preferred orientations close to the
principal meridians are amongst the most sharply tuned, there
is no indication that breadth of tuning shows a linear
increase as a function of deviation of a cell's preferred
orientation from the principal meridians. Examples can be
found, at most orientations, of cells whose breadth of tuning
is within the range shown for cells close to the principal
meridians.

Fig. 4.6 shows symmetry of tuning as a function of the
deviation of a cell's preferred orientation from the principal
meridians. For the great majority of cells, the ratio of
half-widths, at all orientations, falls within the range of
1.0 to 2.0 and the distribution of symmetry values, at all
orientations, is similar.

Fig. 4.4

Distribution of Cells' Preferred Orientations in Relation to
the Principal Meridians.

The histogram shows the distribution of cells' preferred
orientations. The cells' preferred orientations have been
calculated by fitting two regression lines to the flanks of
the cells' tuning curves and determining the intercept values.
The deviation of the preferred orientations from the vertical
and horizontal meridians has then been calculated and the
distribution for the total population of cells has been
constructed.

NUMBER OF CELLS

DEVIATION OF CELL'S PREFERRED ORIENTATION FROM THE PRINCIPAL MERIDIANS (DEG.)
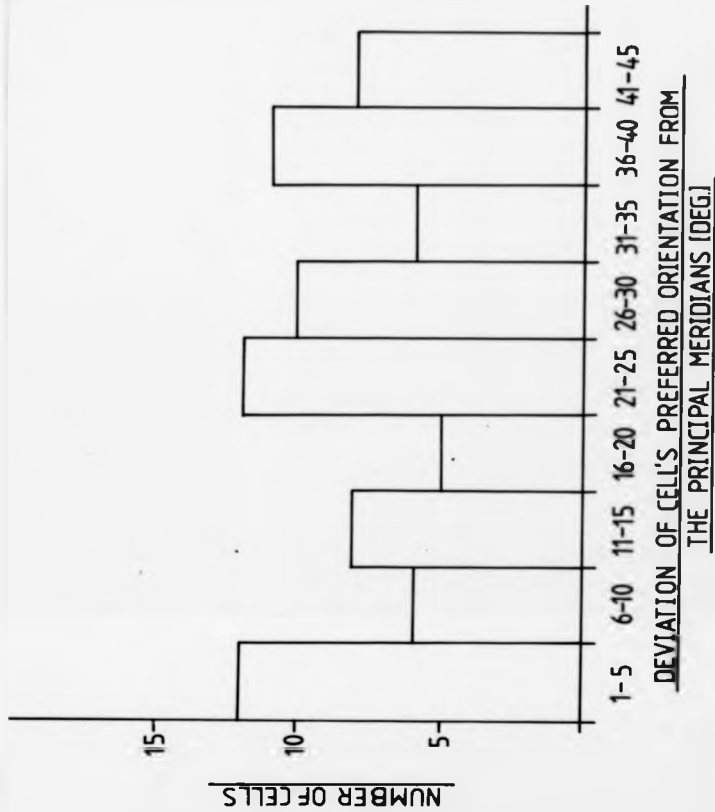
1-5 6-10 11-15 16-20 21-25 26-30 31-35 36-40 41-45

Graph of the Breadth of Tuning for a Moving Contrast Bar as a
Function of Cells' Preferred Orientations in Relation to the
Principal Meridians.

The graph has been constructed to assess whether breadth of
tuning for a moving contrast bar is related to a cell's
preferred orientation. Breadth of tuning is defined by the
total width of the tuning curve at half-height. Breadth of
tuning has then been plotted as a function of the deviation
of the cell's preferred orientation from the principal meridians.

DEVIATION OF CELL'S PREFERRED ORIENTATION FROM THE PRINCIPAL MERIDIANS [DEG]

TOTAL TUNING WIDTH AT HALF HEIGHT [DEG]
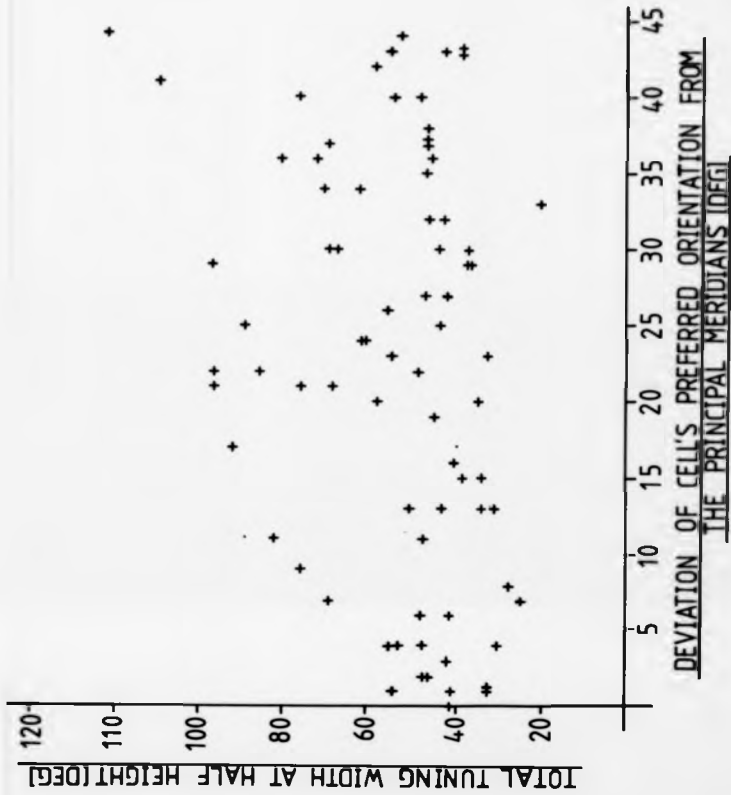
Fig. 4.6

Graph of Symmetry of Tuning for a Moving Contrast Bar as a
Function of a Cell's Preferred Orientation in Relation to
the Principal Meridians.

The graph has been constructed to assess whether symmetry of
tuning for a moving contrast bar is related to a cell's
preferred orientation. Symmetry of tuning is defined by the
ratio of the half-widths at half-height of the tuning curves
following the fitting of regression lines to the flanks.
Symmetry of tuning has then been plotted as a function of the
deviation of the cell's preferred orientation from the vertical
and horizontal meridians.

DEVIATION OF CELL'S PREFERRED ORIENTATION FROM
THE PRINCIPAL MERIDIANS (DEG.)

RATIO OF HALF-WIDTHS AT HALF-HEIGHT
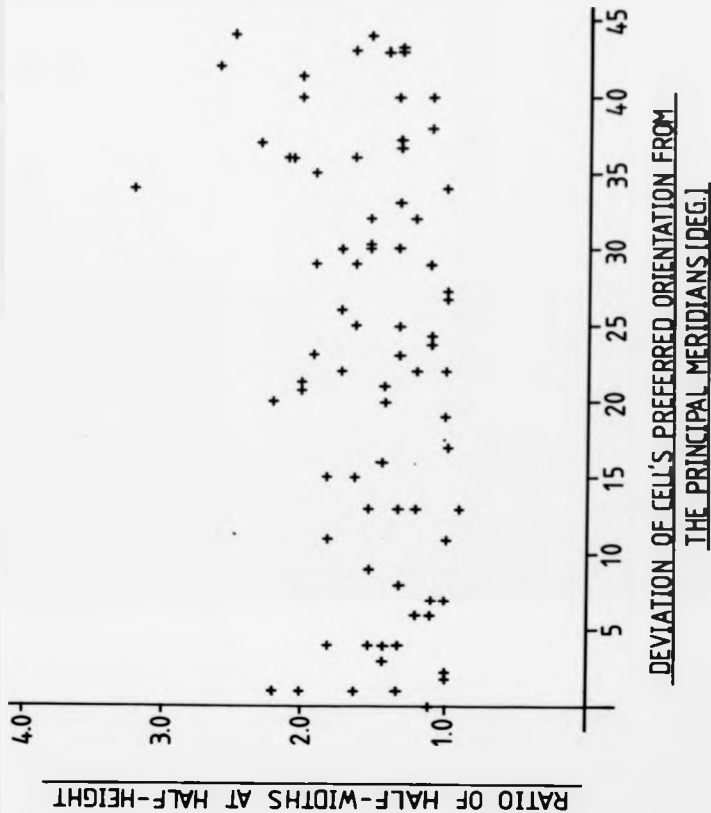
In summary, for the population of complex cells sampled, there is no evidence of an overrepresentation of cells with oblique or horizontal/vertical preferred orientations, nor is there a trend for breadth or asymmetry of tuning for a moving bar to increase as a function of the deviation of a cell's preferred orientation from the principal meridians.

4.8(c) A Comparison of Tuning for Stationary and Moving Contrast Bars

Assessment of tuning for stationary and moving contrast bars was made on a total of 36 cells. Of the thiry-six units 27 gave adequate responses to allow comparison of response for the two stimuli; 17 unimodal units (9 standard, 8 special complex), and 10 bimodal units (9 standard, one special). Units unresponsive to bar flash were distributed amongst both standard and special complex cell groups (4 standard, 5 special). In agreement with previous studies of the simple cell (Henry, Dreher and Bishop, 1974), peak positions in tuning for stationary and moving contrast bars for the majority of <u>complex</u> cells were found to coincide (23/27 units). Similarity of tuning for opposite contrasts of polarity of moving bars was also found for 4 cells tested.

Comparison of breadth of tuning for cells responsive or unresponsive to a stationary flashed bar revealed the former to be more sharply tuned for a moving bar. For the units responsive to a bar flash, the mean breadth of tuning (total width of the tuning curve at half-height) was 49.4 deg. with a range of 26 to 96 deg. The corresponding values for the

cells unresponsive to bar flash were; mean 75.1 deg. with a range of 54 to 113 deg. Comparing the two groups in terms of symmetry of tuning, cells unresponsive to bar flash had a mean symmetry of 1.6 with a range of 1.0 to 2.5. The unit with the broader flank not adjacent to the texture-field tuning curve (176/2), with a symmetry ratio of 0.9, was also a cell unresponsive to bar flash. Cells responding to bar flash had a mean symmetry of 1.5 with a range of 1.0 to 3.2.

Tuning for stationary bars for cells unimodal in their tuning for texture field motion, was consistently sharper than for the same bar in motion (data summary table 3) with a mean difference in total tuning width of 21.4 deg. with a range of 1 to 57. Similarly, for cells showing a bimodal texture response and with asymmetrical bar tuning curves, the same bar presented stationary and flashed produced a sharper and more symmetrical tuning curve. For those cells symmetrical in their tuning for moving bars the corresponding tuning curve for the stationary bar was very similar to that for the moving bar. For the eight standard complex cells with bimodal texture-field tuning showing a response to a stationary flashed bar, the mean difference in the total tuning width between the tuning curves for stationary and moving bars was 9.6, with a range from 0 to 14 deg. The difference in tuning width for the special complex cell showing a bimodal texture-field response was 9 deg. The results for the population of bimodal cells is given in table 4. Expressed as ratios of half-widths, the mean value for symmetry of tuning for stationary bars for the total population of unimodal and bimodal cells was 1.1 (27 units). Comparisons of tuning for

stationary and moving bars for cells unimodal or bimodal in texture-field tuning are illustrated in figs. 4.7-4.10.

4.8(d) Invariance of Tuning for Moving Contrast Bars

Interactions between figure (bar) and ground (texture-field) would clearly bias results. To reduce the possibility of interactions between bar and texture-field, the sample of texture was frequently changed during all experiments and repeated measures of bar tuning against different samples of texture made. Invariance of bar tuning against different samples of texture and over time is illustrated in fig. 4.11. Moving texture-field responses are illustrated in the left-hand figures of the diagram and moving bar responses in the right-hand figures. Between recording of the upper and lower sets of tuning curves, the sample of texture was changed and an interval of one and a half hours elapsed. Though some variability in the texture-field response is apparent, the tuning for the moving bar is constant, despite the different samples of background texture used.

Interesting, in this context, is the cell illustrated in fig. 4.12. The cell was studied over some time, with intervals between the recording of pairs of tuning curves of 30 minutes between the first and second pairs and 1hr. 30 mins. between the second and third pairs. The texture sample was changed between recording each pair of tuning curves. The feature of response which is of particular interest is that a bimodality is present in the tuning for the moving contrast

bar. Separation of the two peaks in the contrast bar tuning
curves is approximately 40 degrees. Tuning for a moving
texture-field, illustrated in the right-hand tuning curves, is
unimodal.

To summarize the main points of the preceding data
analysis, the results of comparison of tuning for stationary
and moving bars would suggest that the asymmetry seen in the
moving bar tuning curve arises from stimulus _motion_.
Identical tuning for stationary and moving bars, reported by
Henry, Bishop and Dreher, (1974) for _simple_ cells, is only
seen in the limited case of cells which show symmetrical
tuning for a moving bar. These cells are found amongst both
cells bimodally and unimodally tuned for texture. Cells
unresponsive to stationary bars, and whose orientation
response is clearly contingent on stimulus motion, are
distributed amongst both standard and special complex cells.
With reference to lamina IV simple cells, units could be
characterized as supra- or infragranular. For the nine cells
unresponsive to bar flash, seven were located in the
infragranular layers and two in the supragranular layers. The
majority were therefore located deep to layer IV. To relate
these numbers to the distribution of cells in the total
population, 27% (21 cells) of the complex cells recorded were
from the supragranular layers and 73% (56) from the
infragranular layers.

TABLE ONE – SYMMETRY OF TUNING FOR MOVING CONTRAST BARS RELATED TO TUNING FOR MOVING FIELDS OF TEXTURE FOR COMPLEX CELLS SHOWING A UNIMODAL RESPONSE TO TEXTURE MOTION. (UNITS:DEGREES).

(A FLANK refers to flank in bar tuning curve adjacent to texture tuning curve).

UNIT NUMBER	178/3	178/4	178/6	176/2	178/7	177/8	177/9	177/11	178/24	178/25	178/26
TEXTURE PEAK	237	236	182	243	72	254	253	23	261	55	8
BAR PEAK	291	268	216	283	90	310	291	30	279	91	21
"A" FLANK 1/2	45	24	49	24	22	53	51	22	45	33	57
"B" FLANK 1/2	23	24	22	27	11	26	26	15	31	21	40
RATIO A:B	2.0	1.0	2.3	0.9	2.0	2.0	2.0	1.5	1.5	1.6	1.4

UNIT NUMBER	177/12	177/13	178/28	178/32	178/33	169/59	177/61	178/65	177/67	178/71	178/73
TEXTURE PEAK	63	255	260	119	187	189	200	334	272	108	220
BAR PEAK	58	276	316	126	217	220	205	371	325	120	247
"A" FLANK 1/2	28	22	81	54	49	28	55	29	31	27	36
"B" FLANK 1/2	18	19	32	26	21	26	35	16	16	17	19
RATIO A:B	1.5	1.2	2.5	2.1	2.3	1.1	1.6	1.8	1.9	1.5	1.9

UNIT NUMBER	169/49	175/5	178/27	169/1	177/10	176/21	177/22	175/23	177/63	182/64	169/45
TEXTURE PEAK	120	253	22	114	183	380	326	146	80	365	260
BAR PEAK	153	4	22	68	154	327	259	94	44	340	229
"A" FLANK 1/2	21	29	49	27	35	54	40	31	31	40	70
"B" FLANK 1/2	21	23	48	23	21	17	42	17	21	18	35
RATIO A:B	1.0	1.3	1.0	1.2	1.7	3.2	1.0	1.8	1.5	2.2	2.0

TABLE ONE CONTINUED - SUMMARY OF TUNING FOR MOVING CONTRAST BARS (UNIMODAL CELLS).

UNIT NUMBER	169/46	177/76	177/77	178/29	177/30	177/31	177/62	177/66	177/68	177/70	177/70
TEXTURE PEAK	254	222	216	14	22	172	222	13	44	177	159
BAR PEAK	248	209	156	16	30	122	209	335	47	163	151
"A" FLANK 1/2	54	24	32	24	39	24	25	25	26	46	50
"B" FLANK 1/2	31	13	28	17	28	20	13	20	18	46	48
RATIO A:B	1.7	1.9	1.1	1.4	1.3	1.2	1.6	1.3	1.4	1.0	1.1

UNIT NUMBER	178/72	178/74	178/54	175/44	169/46	169/47	175/51	176/52	169/55	181/56	178/57
TEXTURE PEAK	295	129	41	318	245	98	249	96	238	236	194
BAR PEAK	324	153	33	165	263	86	326	96	223	290	210
"A" FLANK 1/2	28	24	12	22	35	33	31	25	34	21	46
"B" FLANK 1/2	18	24	9	12	34	23	31	23	22	15	27
RATIO A:B	1.6	1.0	1.3	1.8	1.0	1.4	1.0	1.1	1.6	1.4	1.7

TABLE TWO - SYMMETRY OF TUNING FOR MOVING CONTRAST BARS RELATED TO TUNING FOR MOVING FIELDS OF TEXTURE FOR COMPLEX CELLS SHOWING A BIMODAL RESPONSE TO A MOVING FIELD OF TEXTURE. (UNITS:DEGREES) (A FLANK refers to the greater and B FLANK the lesser of the two sides of the bar tuning curve).

UNIT NUMBER	175/14	175/15	169/16	169/17	169/18	176/19	177/20	169/60	176/34	175/35	169/36
TEXTURE PEAK 1	100	207	4	144	28	204	227	143	103	124	302
TEXTURE PEAK 2	170	302	94	248	90	332	319	233	158	153	38
BAR PEAK	137	255	42	203	53	308	270	188	103	176	347
"A" FLANK 1/2	22	24	42	19	27	25	22	17	20	18	17
"B" FLANK 1/2	17	15	16	15	20	22	20	13	13	12	13
RATIO A:B	1.3	1.6	2.6	1.3	1.3	1.1	1.1	1.3	1.5	1.5	1.3

UNIT NUMBER	175/38	176/39	175/40	175/41	176/42	175/43	175/53	175/50	176/58	178/75	175/37
TEXTURE PEAK 1	53	99	100	212	255	26	342	321	143	114	38
TEXTURE PEAK 2	128	192	174	314	323	99	56	43	216	233	147
BAR PEAK	91	140	137	263	289	53	13	362	156	179	93
"A" FLANK 1/2	24	28	22	13	23	27	24	24	32	22	25
"B" FLANK 1/2	18	27	17	13	23	20	20	24	28	10	18
RATIO A:B	1.3	1.3	1.3	1.1	1.0	1.3	1.2	1.0	1.1	2.2	1.4

TABLE THREE - COMPARISON OF BREADTH OF TUNING FOR MOVING AND STATIONARY CONTRAST BARS.

(Tuning breadth expressed as total width at half-height of the tuning curve fitted with linear regression lines) P=Peak in the tuning curve. W=Width of the tuning curve at half-height. UNITS : DEGREES.

STANDARD COMPLEX CELLS.

UNIT NUMBER	169/1	176/2	178/3	178/4	175/5	178/6	178/7	177/9	177/10	177/11	177/12	177/13
MOVING BAR P	68	283	291	268	364	215	90	291	154	390	58	275
STATIONARY BAR P	NR	NR	297	265	380	96	96	NR	150	396	55	280
MOVING BAR W	50	51	68	48	53	71	33	76	56	37	47	42
STATIONARY BAR W	31	NR	31	26	39	NR	24	NR	34	26	42	40

SPECIAL UNIMODAL CELLS.

UNIT NUMBER	176/21	177/22	175/23	178/24	178/25	178/26	178/27	178/28	178/29	177/30	177/31	178/32	178/33
MOVING BAR P	327	259	94	279	91	23	22	316	16	30	122	126	217
STATIONARY BAR P	NR	NR	91	NR	NR	28	NR	NR	NR	42	121	134	229
MOVING BAR W	326	71	48	76	54	96	96	113	10	67	44	81	70
STATIONARY BAR W	44	NR	39	NR	NR	40	NR	NR	38	27	38	36	32

STANDARD BIMODAL CELLS.

UNIT NUMBER	176/34	175/35	169/36	175/37	175/38	176/39	175/40	175/41	176/42	175/43
MOVING BAR P	103	175	347	93	91	140	137	263	289	53
STATIONARY BAR P	104	179	345	93	81	139	139	265	289	58
MOVING BAR W	33	30	31	43	42	55	39	26	46	47
STATIONARY BAR W	25	26	19	34	30	NR	30	26	32	38

Only one "Special" complex cell with a bimodal texture response responded to a flashed bar.

The corresponding figures for that unit were:-

UNIT NUMBER 175/14 Total tuning width for moving contrast bar : 39 deg. Peak : 137 deg.

Total tuning width for stationary contrast bar : 30 deg. Peak : 140 deg.

(Units marked NR for the stationary bar condition were unresponsive to a flashed bar)

<u>Description of Tuning Curves.</u>

The following convention is followed for this and subsequent
diagrams.   Tuning curves represent the response for a particular
stimulus, for movement in a round-the-clock sequence.   Vertically
upward motion is specified as 0 deg. Each bin shows the response
for each direction of stimulus movement with binwidth set at   ten
degrees.   Direction   was stepped clockwise. The right-most pair
of bins is a calibration signal of 50 spikes/sec. The horizontal
dotted line represents the cell's resting discharge.

<u>FIG 4.7</u>

<u>Comparison of Tuning for Stationary and Moving Contrast Bars for
a Cell Bimodally Tuned for Moving Texture-field with Unequal
Peaks in the Texture-Field Tuning Curve.</u>

Tuning for bar motion is asymmetrical with the broader flank in
bar tuning facing the more prominent peak in the texture-field
tuning curve. Compared with tuning for a moving bar, tuning for
a stationary, flashed bar is sharper and more symmetrical though
peaks are identical for both bar stimuli. For each pair of
responses to a moving contrast bar, i.e. for each of two
opposite directions of motion, there is one common value for bar
orientation. Therefore, whilst the responses to a moving bar are
registered in the two halves of the tuning curve, the responses
to the corresponding stationary bar are contained within one
half. To indicate this equivalence, the stationary bar responses
are replicated over the two halves of the tuning curve in this
and the following three diagrams.

Unit number: 169/36 Standard complex cell from the supragranular
layers.
Receptive field size: 1.8 deg. sq.

Bar dimensions: 8.7 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 1.5 deg./sec.

Calibration Signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

STATIONARY CONTRAST BAR
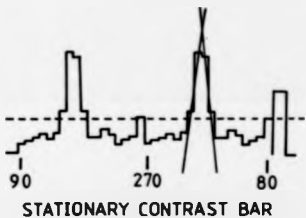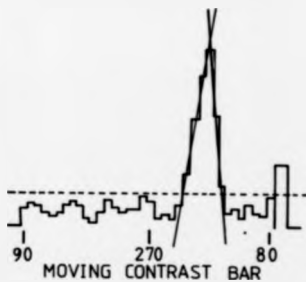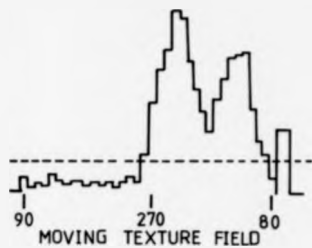
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.8

Comparison of Tuning for Stationary and Moving Contrast Bars for
a Cell Unimodally Tuned for Texture Motion

Tuning for moving bar is asymmetrical with the broader flank in
the tuning curve adjacent to the texture-field tuning curve.
Compared with tuning for moving bar, tuning for a stationary
flashed bar is sharper and more symmetrical. Peak positions for
stationary and moving bars are dissimilar.

Unit number: 178/33 Special complex cell of the infragranular
layers.
Receptive field size: 9.3 deg. sq.

Bar dimensions: 8.5 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 3 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
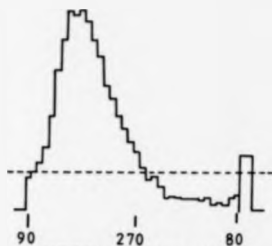
MOVING TEXTURE FIELD

MOVING CONTRAST BAR
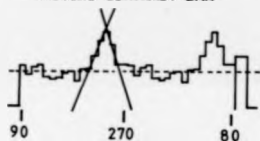
STATIONARY CONTRAST BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.9

Comparison of Tuning for Stationary and Moving Contrast Bars
for a Complex Cell Showing Bimodal Texture-Field Tuning with
Equally Prominent Peaks in the Texture-Field Tuning Curve.

The tuning of this cell for contrast bars is typical of complex
cells with bimodal texture-field tuning with equally prominent
peaks in texture-field tuning. Tuning for a moving contrast bar
is symmetrical. Tuning for the same bar presented stationary and
flashed is identical in breadth and symmetry. As for most cells
showing a response to a stationary bar, peak positions for
stationary and moving bar are identical.

Unit number: 175/41 Standard complex cell of the infragranular
layers.
Receptive field size: 6.7 deg. sq.

Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
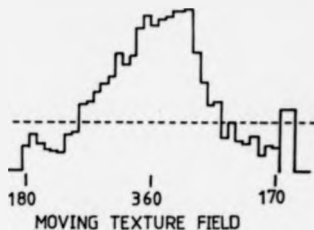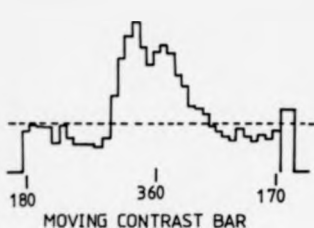Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 1.5 deg./sec.
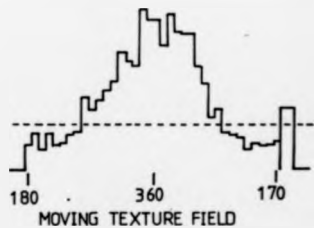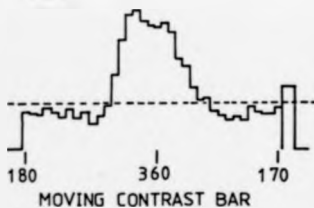
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
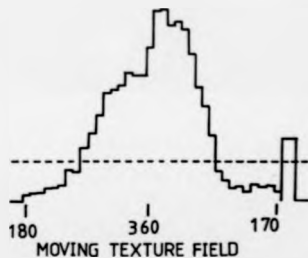Resting discharge is indicated by the dotted line.
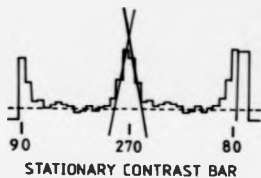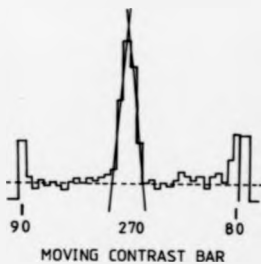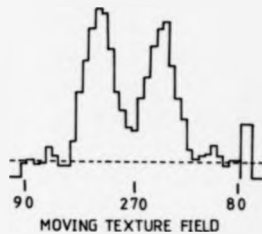
90 270 80
MOVING TEXTURE FIELD

90 270 80
MOVING CONTRAST BAR

90 270 80
STATIONARY CONTRAST BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

Comparison of Tuning for Stationary and Moving Contrast Bars for
a Complex Cell Showing Unimodal Texture-Field Tuning Curve with
Moving Contrast Bar and Texture-field Tuning Curve Peaks in
Register

The symmetrical tuning curve for a moving bar is typical for
units with peaks in tuning curves for moving bar and
texture-field in register. Peaks in the tuning curves for
stationary and moving bars are identical and tuning for the
stationary bar is symmetrical. In comparison to the same bar in
motion, tuning for a stationary bar is sharper.

Unit number: 178/4 Standard complex cell of the infragranular
layers.
Receptive field size: 7.0 deg. sq.

Bar dimensions: 8.9 x 0.5 deg.
Contrast: 0.25 log units above noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 5.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD
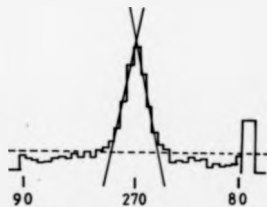
MOVING CONTRAST BAR

STATIONARY CONTRAST BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION (DEG.)

FIG 4.11

Comparison of Tuning for a Contrast Bar Moving Against Different
Samples of Visual Noise

The figure illustrates invariance of tuning for a contrast bar
moving against different samples of stationary visual noise.
Between the recording of the upper and lower pairs of tuning
curves, the sample of texture was changed. An interval of one
and a half hours elapsed between the recording of the two pairs
of tuning curves. Though some variability is seen in the
texture-field response for the two samples of texture, tuning for
the moving contrast bar is invariant despite the changed
background.

Unit number 178/7 Standard complex cell of the supragranular
layers.
Receptive field size: 6 deg. sq.

Bar dimensions:85 x 4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

TEXTURE SAMPLE 1 : TIME 2.55 P.M.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR
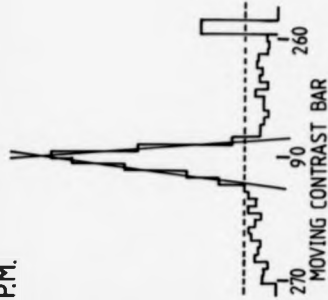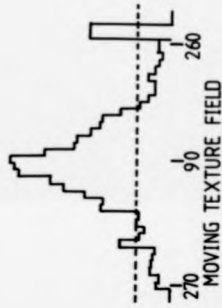
TEXTURE SAMPLE 2 : TIME 4.25 P.M.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR
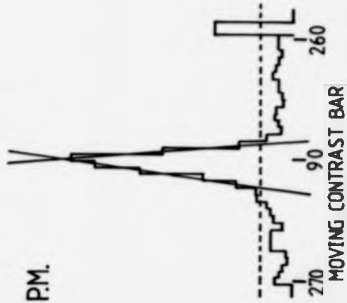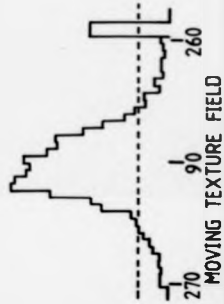
Fig. 4.12 Bimodality of Tuning for a Moving Contrast Bar

The figure illustrates a cell for which a bimodality in tuning
for a moving contrast bar is evident. Each row illustrates
tuning for a moving contrast bar (left-hand side) and the
corresponding tuning curve for moving texture-field (right-hand
side). Between the recording of each pair of tuning curves (A,
B, C) the sample of texture was changed. A bimodality is evident
in tuning for the moving contrast bar with a peak separation of
about 40 degrees. By contrast, the tuning curve for the moving
texture-field is unimodal. These recordings were made over a
period of two hours, with an interval between the recording of
each pair of tuning curves of thirty minutes, between the first
and second pairs, and one and a half hours between the second and
third pairs.

Interval between recordings A and B: 30 mins.
Interval between recordings B and C: 1hr. 30 mins.

Unit number: 176/21 Special complex cell of the infragranular
layers.
Receptive field size: 1.9 deg. sq.

Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Velocity of moving contrast bar and texture-field 4 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

(A)

180   360   170
MOVING CONTRAST BAR

180   360   170
MOVING TEXTURE FIELD

(B)

180   360   170
MOVING CONTRAST BAR

180   360   170
MOVING TEXTURE FIELD

(C)

180   360   170
MOVING CONTRAST BAR

180   360   170
MOVING TEXTURE FIELD

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG]

4.8(e) Tuning of Spots in Comparison with Moving Contrast Bars and Fields of Moving Visual Noise

Tuning for moving contrast spots and contrast bars was compared for 38 cells. In each case, the dimensions of the spots were set at the width of the contrast bar with which tuning was compared and the spot moved through the geometric centre of the receptive field. Spot sizes ranged from 0.3 to 0.5 deg. of visual angle.

Of the 38 cells, 23 were unimodal in their texture response (12 standard and 11 special complex) and 15 were bimodal in their texture field response (8 standard, 7 special complex). The tuning of 3 of the 23 unimodal cells showed identical tuning peak positions for bar and texture. For these cells, the spot peak coincided with that of the contrast bar and texture-field tuning curves. For the other 20, differences in peak position for spot and bar tuning were evident. The mean difference in peak position between the tuning curves for bar and spot was 23.8 deg. with a range of 0 to 65 deg., when all 23 units were included. Data for the bimodally tuned units indicated that, for those units classified as standard complex, 4 out of 8 cells exhibited identical peak positions for bar and spot tuning curves with the other 4 showing differences in peak position of 7, 7, 10 and 14 deg. Two of the special complex cells cells showed co-incidence of spot and bar peaks in the tuning curves the remainder showing a difference in peak position from 11 to 46 degs. with a mean of 26.7 deg.

Collating the results for cells showing symmetrical or asymmetrical bar tuning curves, the following pattern emerged. The results are related to tuning for moving fields of texture. For those cells which were symmetrically tuned for a moving bar, peaks in the tuning curves for spot and bar coincided. In their texture-field response, these neurones were either unimodal with bar and texture field tuning peaks in register, or bimodal cells with equal peaks. Cells asymmetrical in tuning for a moving bar showed a peak shift in the tuning curve for a moving spot. For those cells asymmetrical in their tuning for bar motion, and unimodal in their texture field tuning, the peak shift was in the preferred direction of motion for the texture field. One exception to the rule was found for a cell for which the tuning peaks for bar and texture field were clearly separated but peaks for bar and spots coincided. For cells bimodally tuned for texture motion, with one peak in texture tuning more prominent, a peak shift in the peak of the tuning curve for a spot compared to that for bar motion was seen. The peak shift was in the direction of the prominent peak of the texture-field tuning curve. As would be anticipated from the greater breadth and asymmetry in bar tuning of units of the infragranular layers (Hammond, 1978) peak shift in spot tuning was greater for these cells than their counterparts in the supragranular layers.

Each of these patterns of response is illustrated. Figures 4.13 and 4.14 illustrate units which, asymmetrical in bar tuning, show a peak shift for spot tuning. Cells symmetrical in bar tuning, with no peak shift, or a weak peak

shift in the spot tuning curve, are illustrated in figs. 4.15 and 4.16. Data for the whole population of cells studied are summarized in table 4. As shown by this table, the patterns of behaviour described were independent of the standard/special complex cell classification. As is apparent from the definition of standard and special complex cells (Gilbert, 1977), the former were less responsive to spots. For the majority of neurones, tuning for spot was narrower than tuning for moving texture-field. Comparing tuning for spot and texture-field, greater similarity in breadth of tuning for these two stimuli was found for standard than for special complex cells. The difference in tuning between spot and texture-field was, for standard unimodal cells, 13.7 deg. with a range of 3 to 30 deg. and, for standard bimodal cells, 12.6 deg. with a range of 6 to 21 deg. For special complex cells the figures were; special unimodal mean 17.3 deg. with a range of 0 to 40 deg. and special bimodal cells with a mean of 49.6 deg. with a range of 10 to 81 deg.

Of the three additional units recorded which showed significant end-inhibition, two were bimodal in texture-field tuning and one was unimodal in texture-field tuning. Though distinguished from the other units in the reduction of response magnitude, at lengths beyond an optimal value, the tuning of these units for moving spot, bar and texture-field did not differ from the pattern seen for the larger population. The tuning of the two cells, bimodal in texture-field tuning, for a moving spot, was unimodal.

Henry, Dreher and Bishop (1974) reported that, for all

simple cells and the majority of complex cells, the effect of reducing bar length was to produce no change in the peak of the tuning curve but a broadening of tuning width. A second group of complex cells from the same study, resembling Gilbert's (1977) special complex cells in summatory behaviour, were reported to show similar tuning widths for bars and spots. In this context, breadth of tuning of standard and special complex cells was evaluated. Tuning for standard complex cells exhibited the pattern reported by Henry, Dreher and Bishop (1974) for their majority of complex cells. For the sample of special complex cells investigated in the present study, tuning was invariably broader for spot than for bar. The mean difference was 42.5 deg. with a range of 14 deg. to 109 deg. The existence of Henry, Dreher and Bishop's (1974) second group of complex cells was not confirmed.

4.8(f) Direction Bias and Direction Selectivity for Contrast and Textured Stimuli

"Direction" was distinguished from "axis" in Henry, Dreher and Bishop's (1974) analysis. In the preceding description, little consideration was given to "direction selectivity" or "direction bias" as defined by Henry, Dreher and Bishop (1974). Responses to opposite directions of motion for spot, bar and texture are described in the following analysis.

Of 38 units from which data were recorded for spot, bar and texture motion, 33 were direction-selective in their response to bar, spot and texture motion. The large number of

direction-selective units may reflect a bias in recording from the infragranular layers. The remaining five units showed some degree of bias in response for opposite directions of motion for at least one of the three stimuli.

Two of the units were unimodal in their texture-field response. One unit was direction-selective for bar and spot motion but directionally biased for texture motion at the cell's preferred velocity for bar motion (unit 176/57). The other unit was, at the cell's preferred velocity for bar motion, directionally selective for texture and bar motion but direction biased for spot motion (unit 175/5; fig. 4.17).

From the three units showing a bimodal texture-field response, two units (175/ 35; 175/50) were direction biased for bar but selective for moving texture field and spot. The third unit (176/42) was extensively studied and is illustrated in fig 4.18. At lower velocities, the cell was direction biased for bar motion, and direction selective for texture-field and spot motion. The response to texture-field motion was unimodal at 3 deg./sec. As stimulus velocity increased, direction bias in the bar response increased, with only a small response response in the non-preferred direction at a stimulus velocity of 5 deg./sec. The spot response remained unimodal as velocity was increased. Tuning for texture-field motion became increasingly bimodal while remaining direction selective as velocity was increased. For clarity of exposition, and to emphasise the differences in spot and texture-field tuning, spot tuning at one velocity is shown.

TABLE FOUR – COMPARISON OF TUNING CURVE PEAK POSITIONS FOR MOVING CONTRAST BAR, MOVING SPOT AND MOVING TEXTURE FIELDS (PEAKS DETERMINED FROM THE INTERCEPTS OF LINEAR REGRESSION LINES).

(UNITS: DEGREES).

STANDARD COMPLEX CELLS SHOWING A UNIMODAL TEXTURE FIELD RESPONSE.

UNIT NUMBER	169/1	176/2	178/3	178/4	178/6	178/7	177/8	177/9	177/10	177/11	177/12	177/13
BAR PEAK	68	283	291	268	216	90	310	291	154	30	58	276
SPOT PEAK	63	263	258	252	207	83	257	269	177	31	60	268
TEXTURE FIELD PEAK	114	243	237	236	182	72	254	253	183	23	63	255

SPECIAL COMPLEX CELLS SHOWING A UNIMODAL TEXTURE FIELD RESPONSE.

UNIT NUMBER	176/21	177/22	175/23	178/24	178/25	178/26	178/29	178/30	177/31	177/32	178/33
BAR PEAK	327	259	94	279	91	21	16	30	122	126	217
SPOT PEAK	356	325	103	270	79	1	24	17	150	116	207
TEXTURE FIELD PEAK	380	326	146	261	55	8	14	22	172	119	187

TABLE FIVE - COMPARISON OF TUNING CURVE PEAK POSITIONS FOR MOVING BAR, MOVING SPOT AND MOVING TEXTURE FIELDS. (PEAKS ARE DERIVED FROM THE INTERSECTION OF REGRESSION LINES FITTED TO THE TUNING CURVES). (UNITS : DEGREES).

STANDARD COMPLEX CELLS SHOWING A BIMODAL TEXTURE FIELD RESPONSE.

UNIT NUMBER	176/34	169/36	175/37	175/38	176/39	175/40	175/41	176/42
BAR PEAK	103	347	93	91	140	137	263	289
SPOT PEAK	97	350	91	101	147	139	267	303
TEXTURE PEAK ONE	103	302	38	53	99	100	212	255
TEXTURE PEAK TWO	158	38	147	128	192	174	314	323

SPECIAL COMPLEX CELLS SHOWING A BIMODAL TEXTURE FIELD RESPONSE.

UNIT NUMBER	175/14	175/15	169/16	169/17	169/18	176/19	177/20
BAR PEAK	137	255	42	203	53	308	270
SPOT PEAK	99	244	47	179	98	316	255
TEXTURE PEAK ONE	100	207	4	144	28	204	227
TEXTURE PEAK TWO	170	302	94	248	90	332	319

FIG 4.13

Comparison of Tuning for a Moving Contrast Spot with Moving
Contrast Bar and Texture-field for a Cell Bimodal in its
Texture-field Response

Responses to the three stimuli were recorded at the same
velocity, intermediate in the cell's response range. Tuning for
texture-field motion shows one prominent peak. The broader flank
in the contrast bar tuning curve is on the side adjacent to the
more prominent peak in texture-field tuning. The response to a
moving spot is typical for a cell bimodal in its texture-field
response with unequal peaks in texture-field tuning. The reduced
stimulus length results in a peak shift from that in bar tuning
to the prominent peak in texture-field tuning.

Unit number: 175/15 Special complex cell of the infragranular
layers.
Receptive field size: 8.5 deg. sq.

Bar dimensions: 9 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field
5.5 deg/sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST SPOT

MOVING CONTRAST BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG

Comparison of Tuning for a Moving Contrast Spot with a Moving Contrast Bar and Texture-field for a Cell Unimodal In Its Texture-field Response

Tuning for a moving contrast spot is related to tuning for a moving contrast bar and texture-field. The responses were recorded at the same velocity which was intermediate in the cell's response range. With reduced length, a peak shift is seen with the peak in the spot tuning curve shifted from the peak in bar tuning to the peak in texture-field tuning.

Unit number: 177/31 Special complex cell of the infragranular layers.
Receptive field size: 9 deg. sq.

Bar dimensions: 8.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field
7 deg/sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

250   170   240

MOVING CONTRAST SPOT

250   170   240

MOVING CONTRAST BAR

250   170   240
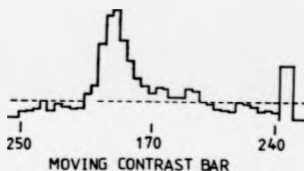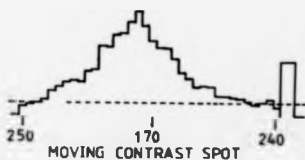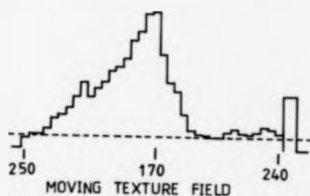
X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]

Comparison of Tuning for a Moving Contrast Spot with Moving
Contrast Bar and Texture-field for a Cell Bimodal in
Texture-field for a Cell Bimodal in Texture-field Response
with Equally Prominent Peaks in the Texture-field Tuning Curve

Tuning for a moving contrast spot is related to tuning for a
moving contrast bar and texture-field. For this cell,
symmetrical in tuning for a moving bar, the peak in tuning for a
spot is close to the peak in the tuning curve for the moving bar.
Though tuning for texture-field motion is bimodal, the spot
tuning curve is unimodal.

Unit number: 175/41 Standard complex cell of the infragranular
layers.
Receptive field size: 6.7 deg. sq.

Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field
3 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING CONTRAST SPOT
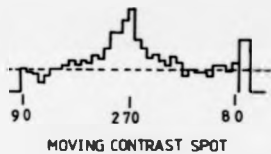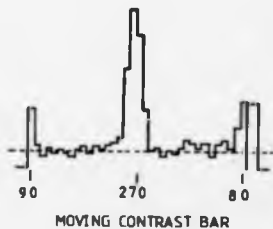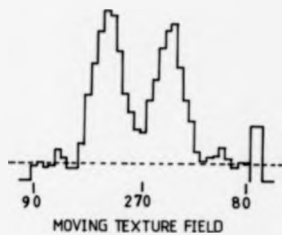
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.16

Comparison of Tuning for a Moving Contrast Spot with Tuning for
a Moving Texture-field and Contrast for a Cell Unimodal in
Texture-field Tuning with Bar and Texture-field Tuning Curve
Peaks in Register

Tuning for a moving contrast spot is related to tuning for a
moving contrast bar and texture-field. Responses were recorded
at the same velocity, intermediate in the cell's response range.
For this unit, as for others with bar and texture-field tuning
curve peaks in register, the peak in the spot tuning curve is
identical to that for bar and texture-field.

Unit number: 177/12. Standard complex cell of the supragranular
layers.
Receptive field size: 4.8 deg. sq.

Bar dimensions: 9.5 x 0.5 deg.
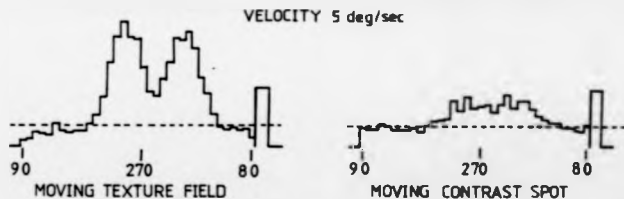Contrast: 0.6 log units below noise background.
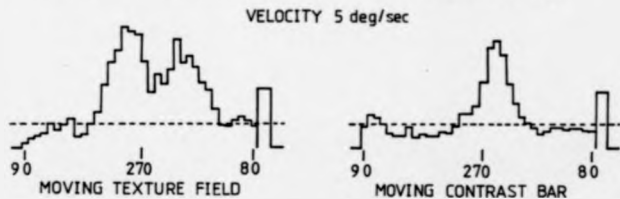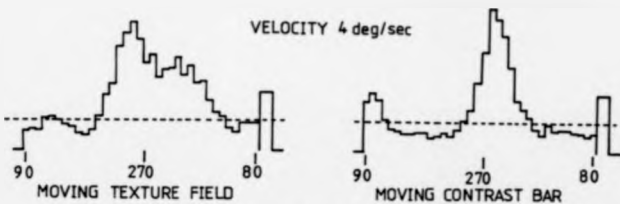Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field
2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR
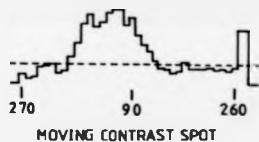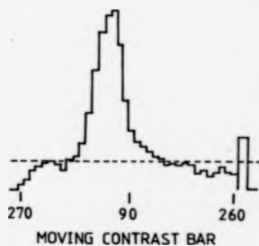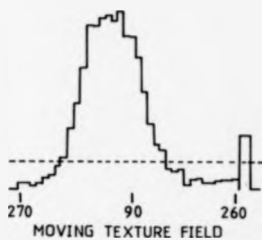
MOVING CONTRAST SPOT

X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]

Comparison of Directional Selectivity and Directional Bias for Moving Texture-Field Contrast Bar and Contrast Spot

The response to opposite directions of motion is illustrated in the tuning curves for moving texture-field, contrast bar and spot. In response to moving texture-field and contrast bar, the cell is direction-selective. By contrast, the response to the contrast spot is direction biased. The tuning curves were obtained at the same velocity, intermediate in the cell's response range.

Unit number: 175/5. A complex cell of the supragranular layers intermediate between classical standard and special complex cells, but with the response to a moving spot clearly less than that to the moving contrast bar.
Receptive field size: 2.1 deg. sq.

Bar dimensions: 8.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
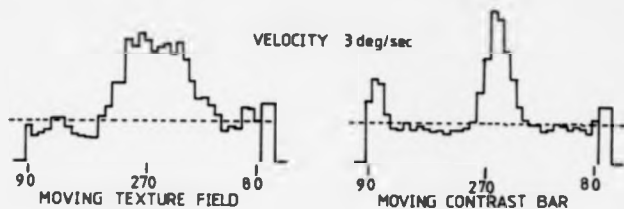Spot dimensions: 0.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field 1.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING CONTRAST SPOT
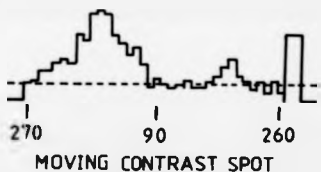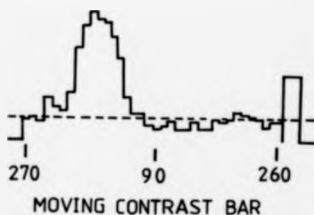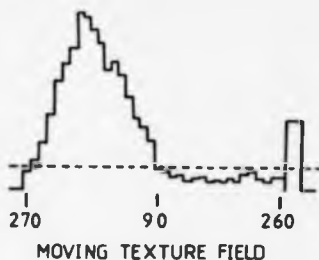
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.18

The Dependence of Direction Bias and Tuning on Stimulus Velocity

The tuning for contrast and textured stimuli at a range of
velocities is illustrated. At low velocities (3-4 deg./sec.),
the cell was direction-biased for bar motion but
direction-selective for moving texture-field and spot. As
velocity increased, the direction bias for bar tuning increased
with reduced response to bar motion in the non-preferred
direction at 5 deg./sec. At low velocities, response to
texture-field motion was unimodal. Increasing the velocity of
texture-field motion produced a bimodal texture-field tuning
curve. The response to the moving contrast spot remained
unimodal and direction-selective at all velocities. For clarity
and to emphasise the differences in spot and texture-field
tuning, spot tuning is illustrated at a high velocity.

Unit number: 176/2. Standard complex cell of the infragranular
layers.
Receptive field size: 6.9 deg. sq.

Bar dimensions: 8 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by dotted the line.

VELOCITY 3 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 4 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 5 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 5 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST SPOT

X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG

4.8(g) Tuning for Moving Spot and Texture Fields as a Function of Velocity

Differences in tuning properties for moving spot and texture-fields were evident when stimulus velocity was varied. For the unit illustrated in fig 4.19, bar tuning was velocity invariant. At a low velocity, (1 deg./sec.), tuning for texture-field motion was weakly bimodal. Comparisons of the spot tuning curve with that for moving texture-field and moving contrast bar, show that the peak in the moving spot tuning curve is shifted from that for the contrast bar towards the prominent peak in the texture-field tuning curve at all velocities used. As velocity was increased to 3 deg./sec. and 5 deg./sec., sensitivity to texture-field motion was depressed in directions optimal for bar motion; with increasing velocity the texture-field tuning curve became progressively bimodal. By contrast, the tuning curve for a moving spot remained unimodal at all velocities.

A cell retaining a unimodal texture-field response at all velocities of texture-field motion is illustrated in fig. 4.20. Comparisons of the peak positions for bar, spot and texture-field tuning curves, at the same velocity, illustrates a common feature of unimodal units with separated peaks for bar and texture-field motion; the peak for spot tuning is shifted from the bar tuning curve peak towards that for texture motion. The feature highlighted in this figure is that, at all velocities, the peak position for the moving spot is shifted from the peak in bar tuning to that of the texture-field.

Comparison of Tuning for a Moving Contrast Spot and Texture-field
at Different Velocities for Complex Cell Typically Bimodal in Its
Texture-field Tuning Curve

The responses to moving texture-field and a contrast spot at a
range of velocities is illustrated. At a velocity of 1
deg./sec., response to a moving texture-field is weakly bimodal.
As velocity is increased to 3 deg./sec. and then to 5 deg./sec.,
the response to texture-field motion is increasingly bimodal. At
the lowest velocity tested, response to texture-field motion is
predictable from tuning for spot. At higher velocities, when
texture-field tuning is bimodal, tuning for moving spot remains
unimodal. Bar tuning was velocity invariant.

Unit number: 177/20. Special complex cell of the supragranular
layers.
Receptive field size: 5.8 deg. sq.

Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
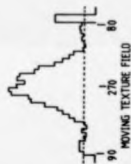Texture-field dimensions: 10 x 10 deg.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
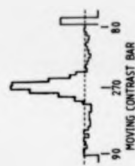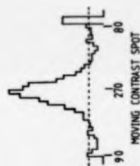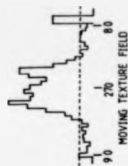
VELOCITY 1 deg/sec   VELOCITY 30deg/sec   VELOCITY 5 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST SPOT
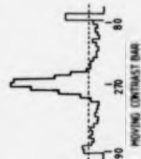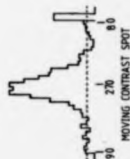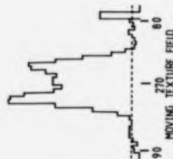
MOVING CONTRAST BAR
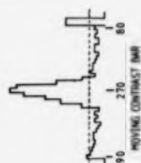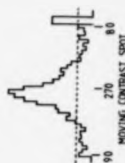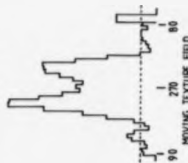
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.20

Comparison of Tuning for a Moving Contrast Spot and Texture-field
at a Range of Velocities for a Complex Cell Unimodal in its
Texture-field Responses

The responses to a moving texture-field and a contrast spot are
illustrated at three velocities. At all velocities tested, the
cell's response to a moving texture-field remained unimodal. In
comparison with tuning for a moving contrast bar, the peak in the
tuning curve for a moving spot is shifted towards the peak in the
tuning curve for the moving texture-field.

Unit number: 177/9 Standard complex cell of the supragranular
layers.
Receptive field size: 9 deg. sq.

Bar dimensions: 8.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocities are indicated in the diagram.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
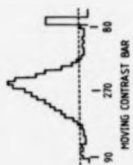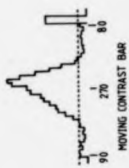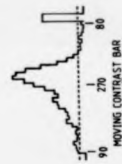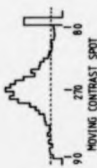Resting discharge indicated by the dotted line.

VELOCITY 4 deg/sec   VELOCITY 6 deg/sec   VELOCITY 8 deg/sec

MOVING TEXTURE FIELD   MOVING TEXTURE FIELD   MOVING TEXTURE FIELD

MOVING CONTRAST SPOT   MOVING CONTRAST SPOT   MOVING CONTRAST SPOT

MOVING CONTRAST BAR   MOVING CONTRAST BAR   MOVING CONTRAST BAR
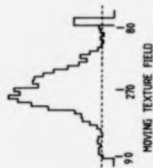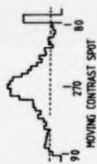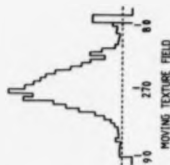
X AXIS OF TUNING CURVES = DIRECTION OF MOTION [DEG.]

An important question is whether changing velocity would alter the shift in peak position in the tuning curve for spot motion. For unit 177/20 the peaks were 259 deg. (at 1 deg./sec.), 256 deg. (at 3 deg./sec.) and 249 deg. (at 5 deg./sec.). Corresponding figures for the other unit 177/9 were 269 deg. (at 4 deg./sec.), 267 deg. (at 6 deg./sec.) and 253 deg. (at 8 deg./sec.). For the third unit 177/31, not illustrated, the figures were 142 deg. (at 4.0 deg./sec.), 150 deg. (at 7 deg./sec.) and 164 deg. (at 8 deg.). For this unit, peak positions for bar and texture respectively were 122 deg. and 172 deg. (at 7 deg./sec.). In summary, increasing velocity produces a shift in the peak position of the spot tuning curve in the direction of the texture-field tuning curve peak.

4.8(h) Tuning for Texture Bars in Comparison with Contrast Bars and Texture Fields

Tuning curves for a texture bar moving across a field of identical texture and equal mean luminance were compared with those for a moving contrast bar and a whole field of texture for 56 units. In every case, a comparison was made of the tuning curve with the texture bar of the same dimensions as a contrast bar optimal for the cell. Additionally, for some units, an extension in the width of the noise bar was made to increase summatory drive or the width of the bar was set at dimensions which appeared to provide an optimal response. For two cells, the contour of the texture bar alone, without the accompanying body of texture was moved across the background texture. This condition is described as a "ghost bar" (see

Hammond and MacKay, 1977). Tuning at different velocities was assessed for three units.

(i) Differences in Sensitivity to Texture Bar Motion

As illustrated for unit 177/12 (fig. 4.21), a cell of the supragragranular layers, all cells were sensitive to the phase of the visual noise sample. Those of the supragranular layers were particularly sensitive to the clustering of elements in the noise sample, as previously reported by Hammond and MacKay (1977) for responsiveness to fields of visual noise. Taking more than one sample of visual noise allowed an estimate of sensitivity to texture bar motion to be made.

Invariably, response to a texture bar was less than that of the cell's responses to a moving contrast bar or moving texture field. Differences in sensitivity to a moving texture bar between complex cells were seen. Several factors contributed to these differences. A primary determinant of responsiveness was receptive field size. As a measure of sensitivity, mean frequency of firing at the preferred direction for texture bar motion was compared with receptive field size (minimum response field). The dimensions of the texture bar were set at those optimal for a contrast bar. For receptive fields of more than 10.5 deg. sq., little modulation of reponse by the texture bar was seen (bar dimensions ranged from 8 x 0.4 deg. to 9.5 x 0.8 deg.). Below that receptive field size, in general, there was a trend for responsiveness to texture bar motion to increase with

decreasing receptive field size (receptive field size ranging from 10.5 to 1.7 deg. sq.). At the extreme ends of the receptive field size range, special and standard complex cells differed in frequency of distribution; the larger receptive field sizes being associated with special complex and the lower end with standard complex cells. There was, however, no clear difference in sensitivity between standard and special complex cells, reflecting the considerable overlap at intermediate receptive field sizes.

Responsiveness was clearly influenced by the tuning properties of the cell. For example, unit 177/10 and unit 169/55 had receptive field sizes of 6.5 and 6.1 deg. sq. respectively, but the response of the second unit was three times that of the first (27 spikes/sec. : 9 spikes/sec.). Comparison of tuning for moving contrast bar and texture field indicated that those neurones most sensitive to texture bar motion were those whose tuning curves for contrast bar and texture-field motion were most similar, typically those neurones of the supragranular layers (e.g. see fig. 4.23) with identical peaks in bar and texture-field tuning curves. Conversely, at the other extreme, one infragranular neurone with well separated peaks for bar and texture tuning showed little sensitivity to texture bar motion. (fig. 4.24). The range of texture-bar responses is illustrated in figs. 4.23-4.27.

Of the fifty-six units only one cell showed an identical tuning curve to the corresponding contrast bar; for this cell tuning remained invariant for two noise bars from different

texture samples. Occasionally, a cell was encountered which
at first appeared to exhibit identity of tuning for these
stimuli but changing the sample of texture brought about a
change in the tuning curve i.e. the response was
phase-dependent. Some cells were unresponsive to texture bars
of the same dimensions as an optimal contrast bar (8 unimodal,
8 bimodal cells). A number of units produced a response to
clusters of elements within the texture bar while showing
little degree of tuning (14 unimodal and 4 bimodal cells).

Some units responded well to texture bars of the same
dimensions of the contrast bar chosen as optimal for the cell.
Characteristically, these were units with a unimodal texture
response with texture field and contrast bar tuning curve
peaks in register (7 units). Four units, unimodal in their
texture field tuning and with dissimilar tuning for bar and
texture field tuning were seen whose responses to texture bars
(of the same dimensions as the corresponding contrast bar)
matched closely the texture-field response, in both peak
position and width of tuning.

For cells showing a bimodal texture field response, two
types of response were seen. Some units, five in total, gave
texture bar reponses identical in form to the cell's texture
field response but reduced in strength. Six units showed a
texture bar response similar to that for the texture-field but
with a plateau in the tuning curve. Whilst there was some
impression that cells with smaller receptive field sizes were
more likely to produce a bimodal response to a moving
texture-bar, it is important to note that no evaluation of

tuning for texture-bar motion, as a function of velocity, for
cells with bimodal texture-field tuning was undertaken.
Differences between cells showing a bimodal texture-field
tuning curve may, therefore, be attributable to differences in
velocity tuning characteristics. Four cells, bimodally tuned
for texture-field motion, showed response to elements within
the texture-bar but produced no clear tuning curve.

(ii) Response to a Dynamic Texture Contour

Response to a dynamic contour was tested on two cells.
The dynamic contour was produced by a bar shaped "window"
through which a second, stationary noise field was visible as
the window was swept to and fro. As the foreground was also
stationary, a stimulus was produced that provided the dynamic
contour of the noise bar moving across the receptive field
(for further details see Hammond and Mackay, 1977). For both
neurones, motion of the dynamic contour produced a small
modulation of response about the resting discharge level. In
neither case did the response to the dynamic contour match the
tuning curve for a moving contrast bar. The tuning of both
units for texture bar motion was similar to the corresponding
moving texture-field tuning curve, though reduced in
amplitude. An example is illustrated in fig. 4.28.

4.8(iii) Temporal Summation with a Moving Texture Bar

Three cells, unimodal in their texture field response,
were tested with a texture bar whose dimensions were set for a
contrast bar optimal for the cell but whose velocity was

varied. A qualitative assessment was first made of the velocity range to which each cell responded to texture-field motion. Within that range, velocity was varied and response to texture field and texture bar was recorded. The data for one cell, in the form of tuning curves for texture-field and texture bar motion are illustrated in fig 4.29. At the lowest velocity tested, there was a weak excitatory response to the moving texture-bar. As velocity increased, there was a small excitatory response at 2 deg./sec., with reduction of response below the level of the resting discharge for the non-preferred directions. When the velocity was increased to 3.5 deg./sec., there was no evidence of an excitatory response but very clear suppression of response below the resting discharge level for a range of directions over which there was a suppression of response to a moving texture-field. The two other units, for which the effect of texture bar velocity was tested, showed similar patterns of behaviour. No data were obtained for response to texture bar motion at different velocities for cells showing a bimodal response to texture field motion.

(iv) Spatial Summation with a Moving Texture Bar

In early experiments, units were encountered giving weak or negligible responses to texture bars of dimensions of a contrast bar optimal for the cell. The increased summatory drive provided by wider texture bars was used to investigate the tuning properties of these cells.

For those cells which were unresponsive to texture bars of dimensions optimal for a contrast bar, the summatory drive

given by increasing the stimulus width was seen to produce an increased amplitude of response. There was, however, no evidence that changing the width of the noise bar changed the range of directions to which the cell responded. An example is illustrated in fig 4.30.

The Dependence of Texture-bar Tuning on Texture Sample

The tuning curves illustrate the dependence of texture-bar
responses on texture sample.   Responses to three texture-bars
formed from different samples of visual noise are illustrated   in
the right-hand curves.   The texture-bars were moved against a
field of stationary visual noise of similar texture and equal
mean luminance.   For comparison, tuning for a field of visual
noise and a moving contrast bar are illustrated on the   left-hand
side.

Unit number: 177/12 Standard complex cell of the supragranular
layers.
Receptive field size: 4.6 deg. sq.

Contrast bar dimensions: 9.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
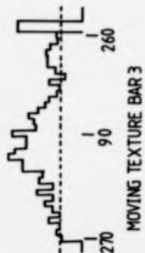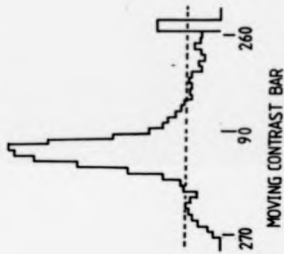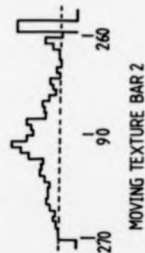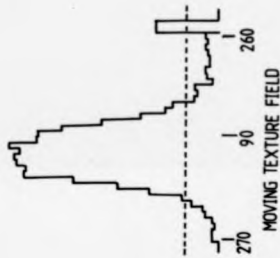Texture-bar dimensions: 9.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for texture-field and texture-bars
2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING TEXTURE BAR 1

MOVING TEXTURE BAR 2

MOVING TEXTURE BAR 3

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.22

Comparison of Tuning for a Texture-bar Moving Across a Field of
Similar Texture and of Equal Mean Luminance with Tuning for a
Moving Contrast Bar and a Moving Field of Texture

Compared to response to a moving field of visual noise or
contrast bar, the response to a moving texture-bar is reduced.
The tuning for texture-bar motion is typical for a cell unimodal
in its texture-field response with peaks in texture-field and
contrast bar in register. Response to texture-bar is strong
compared with units with well separated peaks in tuning for
moving bar and texture-field. The breadth of tuning for
texture-bar is wider than for the contrast bar of equal
dimensions but matches the width of the texture-field tuning
curve. Width of the contrast and texture-bar were set at
dimensions which produced an optimal response to the contrast
bar.

Unit number: 169/49 Unclassified complex cell of the
infragranular layers.
Receptive field size: 3.2 deg. sq.

Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
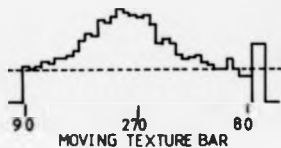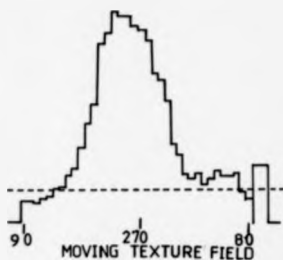Texture-bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and
texture-field 1.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

90   270   80
MOVING TEXTURE FIELD

90   270   80
MOVING CONTRAST BAR

90   270   80
MOVING TEXTURE BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION (DEG.)

Comparison of Tuning for a Moving Texture-bar with Tuning for a Moving Contrast Bar and Texture-field for a Cell Unimodal in Texture-field Tuning with Well-Separated Peaks in Bar and Texture-field Tuning

The response of this cell to texture-bar motion is typical for a cell with a large receptive-field and well-separated bar and texture-field tuning curves. Response to a texture-bar of dimensions producing optimal response to a contrast bar is negligible.

Unit number: 178/6 Standard complex cell of the infragranular layers.
Receptive field size: 11.8 deg. sq.

Bar dimensions: 8.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
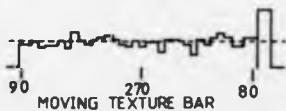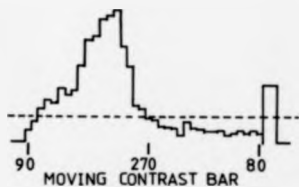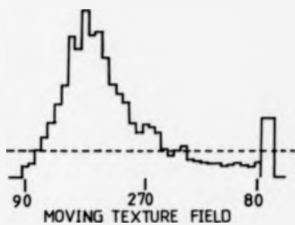Texture-bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-field and texture-bar 3.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING TEXTURE BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

Comparison of Tuning for a Moving Texture-bar with Tuning for
Moving Contrast Bar and Texture-field with a Small Separation
of Tuning Peaks for Bar and Texture-field Motion

The response of this cell to a moving texture-bar is intermediate
between that of the two preceding units illustrated. The tuning
curve for bar motion is contained within the envelope of the
tuning curve for moving texture-field. The peak positions of bar
and texture-field tuning curves are separated by a small distance
compared with many units of the infragranular layers. The
response to texture-bar motion is intermediate compared with the
cells illustrated in figs. 4.22 and 4.23. The tuning curve for
moving texture-bar is broader than that for the moving contrast
bar and broader than that for the texture-field. As with a
number of units, response to the texture-bar is dependent on
clustering of elements in the texture sample.

Unit number: 177/10 Standard complex cell of the infragranular
layers.
Receptive field size: 7.3 deg. sq.

Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and
texture-field 2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR
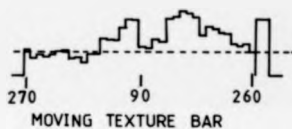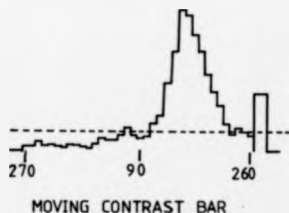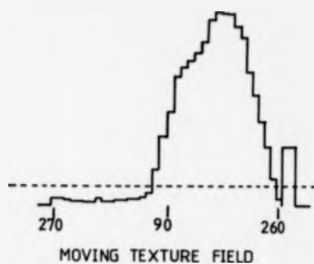
MOVING TEXTURE BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG]

FIG 4.25

Comparison of Tuning for a Moving Texture-bar with Tuning for a
Moving Contrast Bar and Texture-field for a Complex Cell Bimodal
in its Texture-field Tuning

The response of this cell to a moving texture-bar is typical for
one with a large receptive field.   In response to a moving
contrast bar, the cell produces a strong discharge and is sharply
tuned.   To a texture-bar of the same dimensions as the contrast
bar, response is limited to a weak modulation of the resting
discharge.

Unit number: 175/35. Standard complex cell of the infragranular
layers.
Receptive field size: 12.5 deg. sq.

Bar dimensions: 9.0 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9.0 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and
texture-field 3.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING CONTRAST BAR
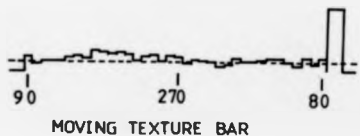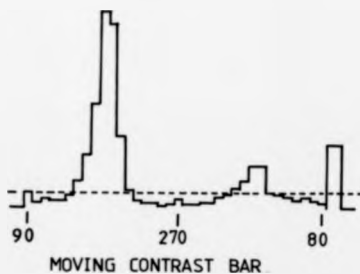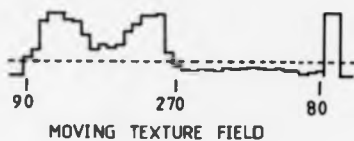
MOVING TEXTURE BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.

FIG 4.26

Comparison of Tuning for a Moving Texture-bar in Comparison with
Tuning for a Moving Contrast Bar and Texture-field for a Complex
Cell Bimodal in its Texture-field Tuning

The tuning curve for moving texture-bar is typical for a complex
cell showing a weakly bimodal tuning curve for texture-field
motion. Response to the moving texture-bar is more broadly tuned
than for the corresponding contrast bar of the same dimensions.
In breadth of tuning, the response to the texture-bar is broader
than that for a moving texture-field. The response to the
texture-bar lacks the depression in sensitivity for directions
optimal for the moving contrast bar seen for some cells with
bimodal texture-field tuning.

Unit number: 175/15. A special complex cell of the
infragranular layers.
Receptive field size: 8.5 deg. sq.

Bar dimensions: 9 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.4 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and
texture-field 3.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

MOVING TEXTURE FIELD

MOVING TEXTURE BAR

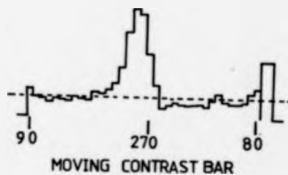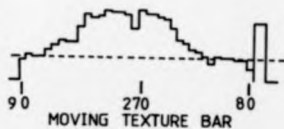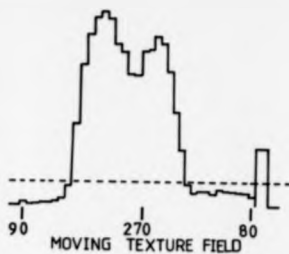MOVING CONTRAST BAR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.27

Comparison of Tuning for a Moving Texture-bar with Tuning for a
Moving Contrast Bar and Texture-field for a Cell Bimodal in its
Texture-field Tuning

The response to a moving texture-field, at a velocity optimal for
bar motion, was bimodal for this cell. The tuning curve for a
moving texture-bar is clearly more broadly tuned than the
corresponding contrast bar of the same dimensions. The tuning
curve for moving texture-bar matches the tuning curve for moving
texture-field in breadth of tuning. The response to the
texture-bar shows some depression of response in directions
optimal for contrast bar motion.

Unit number: 175/14 Special complex cell of the infragranular
layers.
Receptive field size: 3.2 deg. sq.

Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for contrast bar, texture-bar and texture-field
2 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

270   90   260
MOVING TEXTURE FIELD

270   90   260
MOVING CONTRAST BAR

270   90   260
MOVING TEXTURE BAR
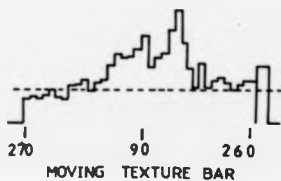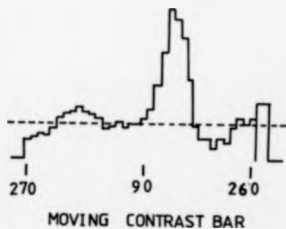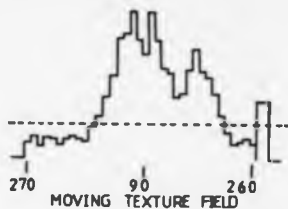
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

Comparison of Tuning for a Moving Texture-bar Contour and
Texture-bar with Tuning for a Moving Contrast Bar and
Moving Texture-field

The response to a dynamic texture contour is illustrated.
Response to the contour is weak and restricted to a small
modulation of response around the resting discharge level. A
greater response is produced by a moving texture-bar. Tuning for
the texture-bar matches the corresponding texture-field response
in breadth, though no depression in texture sensitivity is seen
in the texture-bar response. The dimensions of the texture-bar
were identical to those for a contrast bar. Separation of the
two contours of the moving texture-bar contour equalled the width
of the contrast bar.

Unit number: 169/17. Special complex cell of the infragranular
layers.
Receptive field size: 7.4 deg. sq.

Bar dimensions: 9.2 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9.2 x 0.4 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for contrast bar, texture-bar, texture-contour
and texture-field 3 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
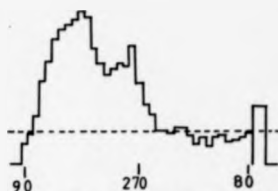
MOVING TEXTURE FIELD
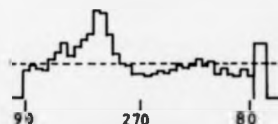
MOVING CONTRAST BAR
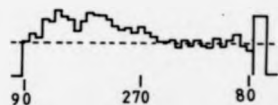
MOVING TEXTURE BAR

MOVING TEXTURE BAR CONTOUR

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

Temporal Summation with a Moving Texture-bar

At a velocity optimal for a moving contrast bar, the cell was
only weakly responsive to a texture-bar of equal dimensions. The
effect of temporal summation is illustrated in the tuning curves
obtained at a range of velocities. At the lowest velocity
illustrated, there is a weak excitatory response to the
texture-bar. As velocity was increased, there was a small
excitatory response to the texture-bar at 2 deg./sec. with
suppression of response below the level of the resting discharge
apparent for non-preferred directions. When the velocity was
increased to 3.5 deg./sec., there was little evidence of an
excitatory response, but very clear suppression of response below
the resting discharge level for a range of directions over which
there was a suppression of response for a moving texture-field.

Unit number: 178/71 An unclassified complex cell of the
infragranular layers.
Receptive field size: 5.3 deg. sq.

Bar dimensions: 9 x 0.6 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.6 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocities for moving texture-field and texture-bar are
indicated in the diagram.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

TEXTURE FIELD   TEXTURE BAR

90   270   80   90   270   80
                  3.5 deg/sec

90   270   80   0   270   80
                  2 deg/sec

90   270   80   90   270   80
                  1 deg/sec
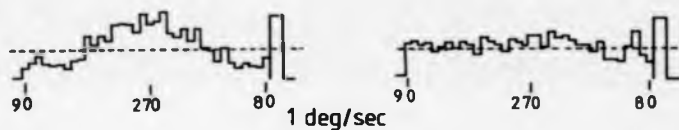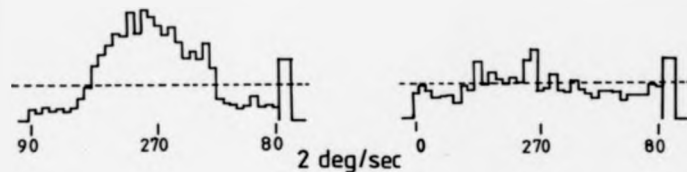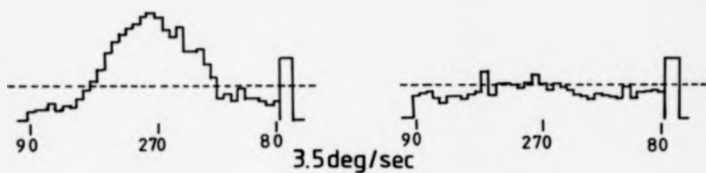
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

FIG 4.30

Spatial Summation for a Moving Texture-bar.

The effect of spatial summation on response to a moving
texture-bar is illustrated. Stimulus velocity was set at that
optimal for a moving contrast bar. The width of the texture-bar
was increased and the tuning curves for each width are
illustrated. Increased stimulus width is associated with
increased response but no change in the range of directions from
which response is elicited.

Unit number: 182/64 An unclassified complex cell of the
infragranular layers.
Receptive field size: 4.6 deg. sq.

Texture-bar dimensions: 8.5 x 0.5 deg.; 8.5 x 0.5 deg.; 8.5 x
0.5 deg.
Contrast bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving texture-field and texture-bar 2
deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.

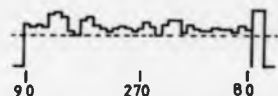BAR PEAK

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING TEXTURE BAR (1.5deg)

MOVING TEXTURE BAR (1.0deg)

MOVING TEXTURE BAR (0.5deg)
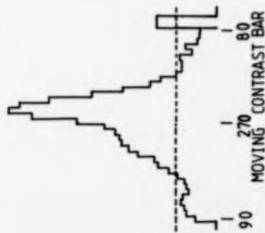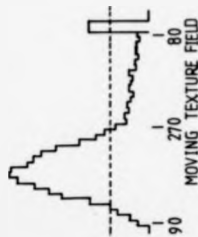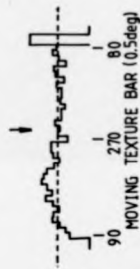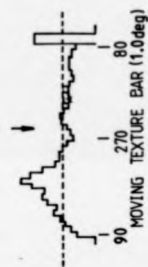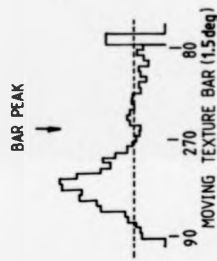
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]

CHAPTER FIVE: Implications of the Tuning of Complex Cells for
 Contrast and Textured Stimuli for Models and the Role of the
Complex Cell in Visual Analysis

5.1 An Overview

The main findings of the experimental investigation can be
summarized.   Tuning of complex cells for a stationary, flashed
bar has poor predictive value for response to moving stimuli;
typically, tuning for a stationary bar is sharper and more
symmetrical than the same bar in motion and preferred direction
for a moving spot is not orthogonal to preferred orientation
for a stationary bar. Preferred direction for a moving
texture-field can be predicted from the preferred direction for
a moving spot. Features of texture-field tuning due its
spatial extent are breadth of tuning and bimodality.
Comparison of tuning for a moving texture-bar with tuning for a
moving contrast bar and texture-field indicates that, in the
absence of luminance cues, complex cells are sensitive only to
texture motion. Implications of these findings for models for
the role of intracortical inhibition in the generation of
tuning properties and for the role of the complex cell in
visual analysis are discussed.

The findings that tuning for a stationary bar is sharper
and more symmetrical than the same bar in motion and that
preferred direction for a spot is not orthogonal to preferred
orientation for a stationary bar are reviewed in the context of
Goodwin and Henry's (1975) model for direction selectivity.   A
functional interpretation is given to the asymmetry in tuning

for a moving bar. The present study has established that the degree of asymmetry in bar tuning is unrelated to the complex cell's preferred orientation but arises from bar motion. The greater asymmetry in tuning for a moving contrast bar of complex cells compared to simple cells, it is argued, reflects a functional difference which may be related to the distinct role of the complex cell in visual analysis.

Features of the complex cell's tuning curve for texture-field motion attributable to spatial and temporal factors are considered. Comparison of tuning for spot and texture-field is interpreted to be consistent with the view that bimodality of texture-field tuning arises from an interaction between orientation and direction selective mechanisms. The functional implication of the absence of a contour response by complex cells to a moving texture-bar is evaluated in the context of Hubel and Wiesel's model for form representation by contour analysis.

The role of the complex cell in visual analysis is discussed and the proposition that the complex cell has a distinct role is considered. The tuning properties of complex cells for contrast and textured stimuli reported in the present study are related to the role of the complex cell in visual analysis. A starting point for the discussion is a review of models for the role of the striate cortex in the representation of form. "Feature extraction" and "population coding" models are reviewed. The feature-extraction model of Hubel and Wiesel (1962, 1963) is rejected on the basis that (1) the tuning properties and receptive field structure of the single cell do

not correspond to the requirements of a feature-extraction
model and (2) intracortical connectivity is incompatible with a
serial, feature-extraction role. A population coding model of
representation is adopted and the roles that simple and complex
cells might play in population coding considered. A role for
complex cells in the analysis of moving objects is established.
Two important conclusions are reached from the discussion; (1)
that the asymmetrical coupling conferring on complex cells
their direction selectivity also provides a compensation for
the distortion of an object associated with its movement and
(2) the perception of form of a moving texture-bar under
conditions in which complex cells respond only to texture
motion prescribes a role for direction-selective units in the
representation of form.

5.2 The Tuning of Complex Cells for Contrast Stimuli

For most striate cortical neurones, the tuning curve for a
moving bar is asymmetrical (Hammond and Andrews, 1978b). The
degree of asymmetry of bar tuning does not increase with
recording depth in penetrations normal to the cortical surface
(Lee, Heggelund, Hulme and Creutzfeldt, 1977; Hammond, 1978).
Areal differences between A.17 and A.18 in asymmetry of tuning
have been reported (Hammond and Andrews, 1978b) which are
consistent with known areal differences in the extent of
horizontal anisotropies of horizontal fibres (Creutzfeldt,
Garey, Kuroda and Wolff, 1977). Asymmetries are not therefore
a byproduct of damage to the fine intracortical wiring with
electrode advance. In the present study, tuning for a
stationary contrast bar was seen to be sharper and more

symmetrical than for the same bar in motion; asymmetries in
bar tuning arise from stimulus motion.

Conditions of stimulus presentation cannot have
contributed to the result. For the simple cell, there is
evidence for figure/ground interactions between a contrast bar
and a textured background (Hammond and Mackay, 1978; Hammond
and MacKay, 1981). The importance of a homogeneous background
for obtaining a flash response from simple cells has been
reported (Emerson and Gerstein, 1977). Hammond and Mackay
(1981) found that moving a field of visual noise in synchrony
with a contrast bar depressed bar response in 70% of simple
cells. By contrast, Hammond (1978) found that the presence of
a stationary background of visual noise did not influence
tuning for a moving contrast bar for his sample of complex
cells. In the present study, interactions between moving bar
and stationary texture were not found.

Complex cells are not only more broadly tuned than simple
cells (Henry, Dreher and Bishop, 1974; Watkins and Berkley,
1974; Albus, 1975; Hammond and Andrews, 1978b; Leventhal and
Hirsch, 1978; DeValois, Yund and Hepler, 1982) but also more
asymmetrical (Henry, Dreher and Bishop, 1974; Hammond and
Andrews, 1978b) in tuning for a moving bar. The possibility is
raised that this represents a functional difference in tuning
between simple and complex cells. This interpretation is made
in discussion of the role of the complex cell in visual
analysis. It is therefore important, at this stage, to rule
out the possibility that the greater asymmetry of tuning of
complex cells is artefactual. Deviations from linearity of the

tuning curve for moving bar are associated with broadly tuned
units (DeValois, Yund and Hepler, 1980). It should be
emphasised, as is illustrated in the tuning curves for
comparisons of tuning for stationary and moving contrast bars
(chapt. 4) that asymmetries of bar tuning are found for
complex cells of a broad range of tuning widths.

The suggestion of Rose and Blakemore (1974) that tuning
width is inversely related to angular distance from the
vertical and horizontal meridians raises the possibility that
asymmetrical tuning is related to preferred orientation. The
proposal was made by these authors for simple but not complex
cells. In the present study, degree of asymmetry was not found
to be related to preferred orientation, confirming Rose and
Blakemore's reports for the complex cell. It was argued
earlier (chapt. 3) both that tuning width is unrelated to
preferred orientation (Wilson and Sherman, 1976; Gilbert,
1977) and that cells with preferred orientations around the
vertical and horizontal meridians are not over-represented
(Rose and Blakemore, 1974; Finlay, Schiller and Volman, 1976;
Wilson and Sherman, 1976; Poggio, Doty and Talbot, 1977). An
over-representation of cells tuned to the vertical/horizontal
or oblique was not found in the present study nor was a
dependence of tuning width on preferred orientation.

Henry, Bishop and Dreher (1974) made no evaluation of
tuning of complex cells for stationary and moving contrast
bars. For simple cells, identical tuning for the two stimuli
was reported. The finding in the present study, that complex
cells symmetrically tuned for moving bar show similar tuning

for a stationary bar suggests that Henry, Bishop and Dreher's (1974) results for simple cells might be a consequence of sampling from symmetrically tuned units. The recent study by Heggelund and Moors (1983), with a much larger sample of simple cells, demonstrated that simple cells asymmetrically tuned for bar motion are more sharply and symmetrically tuned for a stationary bar. The discrepancy between Henry, Bishop and Dreher's (1974) study and investigations of receptive field structure with stationary and moving contrast bars by Benevento, Creutzfeldt and Kuhnt (1972), Creutzfeldt, Kuhnt and Benevento (1974), Innocenti and Fiore (1974) and Fries and Albus (1976) may therefore be resolved. The possibility exists that differences in the tuning properties of simple cells between Henry, Bishop and Dreher's (1974) and Heggelund and Moors (1983) studies may reflect sampling from different populations of simple cells differing in morphology and connectivity.

On the basis of the present study of complex cells and of the strong support given by Heggelund and Moors (1983) study for Rose's (1977) and Hammond and Andrews' (1978b) findings of sharper and more symmetrical tuning for stationary than moving bars for simple cells, it can be concluded that the direction selectivity of both simple and complex cells cannot be accounted for by the spatial organization of the receptive field mapped with a stationary, flashed bar rotated symmetrically about the cell's receptive field centre. However, the degree of asymmetry of complex cells' tuning for moving bars is greater than for simple cells, suggesting a functional difference.

Henry, Bishop and Dreher's (1974) study of simple cells indicated that preferred direction for a moving spot is orthogonal to preferred orientation for a stationary bar. Also, these authors reported that, for a population of five complex cells, preferred direction of a moving spot was identical to that for a moving bar. The present study does not contradict these findings but suggests they have limited validity in describing complex cells' tuning characteristics. Only those cells symmetrically tuned for bar motion showed identical preferred direction for spot and moving bar with preferred direction for spot orthogonal to preferred orientation for a stationary bar. Directional bias could not be predicted from tuning for a stationary bar. Given the complex non-linearities of the length-response curve (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977; Hammond and Andrews, 1978c) one question for future investigation is the contribution of interactions within and between the component parts of the receptive field in the shift in preferred direction with bar length.

In one aspect, the present study is at variance with Henry, Bishop and Dreher's (1974) study. The existence of those authors' second group of complex cells, for which reduced stimulus length brought reduced response but no change in breadth of tuning was not confirmed. Their result was probably a consequence of deriving tuning curves over a limited range of orientations in their study.

5.3 Implications for Models

In the earlier discussion of models for the role of intracortical inhibition, it was suggested that insufficient data were available for evaluation of Goodwin, Henry and Bishop (1975) model for direction selectivity; Goodwin, Henry and Bishop (1975) made no evaluation of stationary flash and movement components in response to a moving contrast bar and Henry, Bishop and Dreher's (1974) data were based on symmetrically tuned units.

The validity of Goodwin, Henry and Bishop's (1975) model can be assessed on two levels; the descriptive level and at the level of mechanism. Earlier evaluation of the model focused on mechanism. At that stage, it was argued that assumptions derived from Hubel and Wiesel's (1962, 1963) and Bishop's (Bishop, Coombs and Henry, 1971b; Bishop, Coombs and Henry,1973) models, of convergence of afferent input and a fixed spatial relationship between intracortical inhibition and afferent excitation, are untenable. Also, it was established that the simple cell is not invariably the recipient of input from LGN cells showing linear summation. Goodwin, Henry and Bishop (1975) attempted an explanation of simple cell's direction selectivity from assuming the properties of intracortical inhibition derive from the spatial organization and summatory properties of the geniculate input to the cell.

Goodwin, Henry and Bishop's (1975) model had its antecedant in Rodieck and Stone's (1965) analysis of response by retinal ganglion cells to moving stimuli. Rodieck and Stone

(1965) reported that the response to a moving spot was "directly correlated with the gradient of the receptive field defined by flashing lights" (i.e. spots). By making the assumptions of (1) a constant time course for a cell's responses to a stationary flashing spot stimulus, whatever its position in the receptive field and (2) a linear summation of influences reaching it from different parts of the receptive field, its responses to various moving stimuli (spots and bars of various dimensions) would be predictable from its sensitivity profile. This analysis provided the basis for Goodwin, Henry and Bishop's (1975) suggestion that the direction selectivity of simple cells might be predictable from the sensitivity profile mapped with a stationary flashed bar. Linearity of summation and a constant time course for inhibition were assumed; intracortical inhibition would reflect the properties of the afferent input and afferent input would be provided by cells showing linear summation.

Goodwin, Henry and Bishop's (1975) model fails not only at the level of mechanism but also at the descriptive level. Since, in the present study, preferred direction for a moving spot was seen to change as a function of velocity, the complex cell receptive field must reflect temporal as well as spatial factors (c.f. also Hammond and Reck, 1980 in the context of the dependence of texture-field tuning on velocity). As revealed in both physiological and anatomical studies (chapter two), most, if not all, complex cells receive intracortical excitatory inputs with many complex cells additionally receiving a direct excitatory input from the LGN. The complex cell receptive field comprises components from intracortical

inhibition which are not in a fixed spatial relationship to the excitatory input.

Contained within the model of Goodwin and Henry (1975) was the assumption that direction-selective inhibition is initiated by a stationary edge, whilst the study of Henry, Bishop and Dreher (1974) provided evidence that the receptive field profile mapped with a stationary bar rotated around the geometric centre of the receptive field is identical to the receptive field structure determining the tuning curve for a moving bar. The present study indicates that the component of the receptive field mediating the direction selective response to a moving bar is not reflected in the receptive field element mapped with with a stationary bar rotated around the cell's receptive field geometric centre. Though the asymmetry in tuning for a moving bar arises from bar motion, the result does not demonstrate a dependence on temporal factors independent of the spatial organization of the receptive field.

Both Goodwin, Henry and Bishop (1975) and Schiller, Finlay and Volman, (1976) assumed each cell to have a single preferred direction for stimulus motion. Functionally, such tuning characteristics would support a feature extraction model of representation; the single cell would signal movement in a particular direction. Not only preferred direction for bar and texture differ (Hammond 1978 and subsequently), but also reduction of stimulus length produces a change in preferred direction. Such tuning behaviour is incompatible with a feature-extraction model but consistent with a population coding model of representation; the tuning properties of

complex cells depend on the configurational properties of the stimulus.

5.4 The Tuning of Complex Cells for Textured Stimuli

Though moving fields of visual noise provide a stimulus free from orientation, a complicating factor in interpreting the tuning curve for moving texture-field arises from the spatial extent of the stimulus. A comparison of tuning for spot and texture-field is interesting in this context. Tuning for spot has a high predictive value for preferred direction for texture-field motion; for cells unimodal in texture-field tuning at all velocities and for bimodal cells at low velocities. For cells bimodal in texture-field tuning at higher velocities, spot tuning remains unimodal and shifts to the prominent peak in texture-tuning with increased velocity.

In the discussion of the bimodality of texture-field tuning, two possibilities raised by Hammond (Hammond, 1978; Hammond and Reck, 1980; Hammond and Smith, 1983) were considered plausible interpretations for the origin of the bimodality. These were that the bimodal tuning is a product of the direction mechanism alone or that it arises from an interaction between orientation and direction selective mechanisms. In the framework of Goodwin, Henry and Bishop's (1975) model for direction selectivity one would predict bimodal spot tuning as a product of a bipartite spatial division of the receptive field.

Bishop, Kato and Orban (1980) reported bimodal spot tuning

for a cell bimodal in texture-field tuning. In one respect only is the present study in agreement with Bishop, Kato and Orban's; reduction in bar length produces a shift in preferred direction. Bimodal spot tuning curves were seen in no case. Bishop, Kato and Orban's (1980) result was based on a complex cell with marked end-inhibition. A possible explanation for the discrepancy may be that complex cells with marked end-inhibition differ in their tuning properties.

Early reports suggested differences in direction selectivity of complex cells with and without end-inhibition (Kato, Bishop and Orban, 1978; Orban, Kato and Bishop, 1979ab). Also, Sillito (1977) has reported contrasting differences in the effect of bicuculline on Type I complex cells of lamina III and hypercomplex cells of the same lamina. Direction selectivity of Type I cells was eliminated following the iontophoretic application of bicuculline but the direction selectivity of hypercomplex cells from layer III was unaffected. Sillito (1977) interpreted this to suggest the possibility of differing synaptic organization underlying the directional specificity of the two types of cell. However, as Bishop, Kato and Orban (1980) themselves found, direction-selective and end-inhibition are derived from separate mechanisms.

Bimodal tuning for spot would imply a bipartite spatial division of the receptive field, a result which would be surprising given the unimodal tuning for texture of bimodal cells at low velocities (Hammond and Reck, 1980a, b). In the present study, in addition to the population of complex cells

recorded, three complex cells with significant end-inhibition were recorded. Two of these cells were bimodal in texture-field tuning. Both showed unimodal spot tuning curves. In summary, Bishop, Kato and Orban's (1980) report of bimodal spot tuning is without support.

On the basis of comparison of tuning for spot and texture-field motion it is reasonable to suggest that cells have a single preferred direction for texture motion and depression of texture sensitivity in the tuning curve for cells showing bimodal tuning arises from an interaction between orientation and direction selective mechanisms. It remains problematical for such a view (c.f. Hammond and Smith, 1983a, b) that bimodal texture-tuning persists at velocities beyond the cut-off velocity for bar response. A second problem is that some cells show identical preferred direction for spot and bar motion but that these cells are distributed among cells unimodal and bimodal for texture tuning. A functional diversity is suggested, as is implied by the studies of Hammond and Smith (1983a,b) that some complex cells respond to the relative motion of bar and texture whilst others respond to the bar regardless of the context in which motion occurs. Connectivity differences remain obscure.

Comparisons of tuning for moving texture-bar with moving contrast bar and texture-field were undertaken in the context of Hubel and Wiesel's hypothesis of form representation by contour-selective neurones. The study reported here has shown that whilst complex cells differ in sensitivity to moving texture-bars, they are uniform in tuning properties; complex

cells do not respond to the dynamic contour of a moving texture-bar.

Hammond and MacKay (1977) reported that the majority of complex cells are less sensitive to texture-bar motion than to a contrast bar of optimal dimensions for the cell and a moving texture-field. Differences in preferred direction for texture and contrast bars were reported in the same study. These findings were confirmed. The present study extends the work of Hammond and MacKay in providing a systematic quantitative evaluation of tuning for a moving texture-bar with contrast bar and texture-field.

For cells unimodal in their texture-field tuning, tuning for moving texture-bar can be simply described. In both peak position and breadth of tuning, texture-bar tuning matched the cell's tuning for moving texture-field. In the limited case of cells with identical peaks for texture-field and contrast bar tuning curves was preferred direction for texture-bar identical to that for contrast bar. Breadth of texture-bar tuning, however, matched the texture-field curve.

Complications arise in the case of cells bimodally tuned for texture motion because of depressed sensitivity to texture motion for directions optimal for contrast bar motion. Interactions between orientational and directional mechanisms were evident in the bimodal response to a texture-bar seen for some neurones. The velocity dependent response to a moving texture-bar was not investigated for bimodal cells. Several observations rule out the possibility that cells bimodal in

texture-field tuning respond to the texture-bar contour. Given the number of units from which data were collected, some evidence of response to the texture-bar contour, even if reduced in amplitude, would have been seen. More directly, many units produced a tuning curve, matching in breadth the tuning curve for moving texture-field, with no suppression of response in directions optimal for bar motion.

The conclusion from comparisons of tuning for moving texture-bar with moving contrast bar and texture-field is that, given certain limitations of spatial summation, complex cells are uniform in tuning; in the absence of luminance cues, complex cells are responsive only to texture _motion_. Support for the conclusion is given by the absence of an orientation-selective response to a dynamic contour. The result indicates that the representation of form cannot be achieved solely by contour detectors.

Effects of spatial and temporal summation with a texture-bar produced several interesting results. It is important to emphasise that reducing or broadening the texture-bar width brought no transition from an edge response, as seen with the contrast bar, to a purely directional response as seen with a texture-field. Another feature seen with broadening of the texture-bar was that the range of directions to which the cell responded did not change with stimulus width; in the conceptual framework of Barlow and Levick (1965), there was no evidence of recruitment of "sub-units".

Two aspects of experiments concerned with temporal

summation with texture-bars of dimensions optimal for a contrast bar warrant discussion. Firstly, it was clear that one could not "trade-off" temporal for spatial summation. A cell might be unresponsive to a bar of dimensions optimal for a moving contrast bar and broadening of the texture-bar's width would produce an excitatory response. Maintaining the same dimensions for the texture-bar at those optimal for a contrast bar, but increasing stimulus speed, did not produce an excitatory response from the units tested. By contrast, increased stimulus velocity was accompanied by suppression of response in directions in which suppression of response was seen in the texture-field tuning curve. These observations cast doubt on Bishop, Kato and Orban's (1980) observation for complex cells that inhibition in the non-preferred direction is augmented by the same stimulus parameters that increase the excitatory response in the preferred direction.

Differences in Tuning Properties Between Different Classes of Complex Cells

MacKay (1976), commenting on the concept of the columnar organization of orientation in the striate cortex, suggested that, given a wider range of stimuli, a wider diversity of functional properties/trigger features between cells showing the same orientation preference may be seen. Potentially, a combination of contrast and textured stimuli provides an opportunity for investigating the functional diversity of complex cell sub-groups.

The classification of complex cells has primarily been

based on properties of summation along the "orientation axis". It is an unresolved question whether this property indicates separate roles for "standard" (including B cells) and "special" complex cells. Laminar differences in distribution of these cell types does suggest differences in afferent and intracortical connectivity and potentially distinct roles.

There is some evidence to suggest that "standard", "special" and B cells differ in geniculate input. Tanaka (1983) reported that "special" cells receive only Y cell input but "standard" complex cells receive both Y and X fibre input. Henry, Mustari and Bullier (1983) reported that B cells receive only W input. The association, suggested by Tanaka (1983), of a differential input to standard and special complex cells with the summatory properties of those two cell groups would suggest a link between, if not a dependence on, summatory behaviour and afferent input which is, at best, unproven and difficult to reconcile with the particular connectivity scheme suggested. Patterns of intracortical connectivity suggest separation of intracortical pathways between standard and special complex cells; lamina VI "standard" complex cells receptive field structure is principally determined by input from lamina V "standard" complex cells (Gilbert and Wiesel, 1979, 1981). Anatomical and physiological evidence has revealed a prominent pathway from lamina III to lamina V potentially linking "standard" and "special" complex cells of lamina III with their counterparts in lamina V (Creutzfeldt, Garey, Kuroda and Wolff, 1977; Lund, Henry and Harvey, 1979; Mitzdorf and Singer, 1978; Gilbert and Wiesel, 1979, 1981). However, there is no evidence for a segregation of pathways such that lamina III

"standard" complex cells contact lamina V "standard" complex cells and "special" complex cells in lamina III provide the exclusive supragranular input to lamina V "special" complex cells.

Segregation of outputs of "standard", "special" and B cells is suggested by the selective input from B cells to the Clare-Bishop area (Henry, Lund and Harvey, 1978), that lamina VI complex cells are exclusively "standard" complex (Gilbert and Wiesel, 1981) and from the early report that "special" complex cells provide the striate cortical input to the superior colliculus (Palmer and Rosenquist, 1974). However, Sillito reported differences within the standard complex group in the derivation of their orientation selectivity (Sillito, 1979). Also, Harvey (1980) has reported "standard" as well as "special" complex cells project to the superior colliculus.

The results of the present investigation emphasise the independence of many tuning properties of the "standard"/"special" dichotomy. It is clear that "standard" and "special" complex cells are not distinguished by many aspects of response. Both "standard" and "special" complex cells are distributed among cells unimodal and bimodal in texture-field tuning, as Hammond (1978) has also reported. The tuning of both categories of cell for texture-bar motion showed an identity to the cell's texture field response. Not only are some "special" complex cells unresponsive to bar flash but also some "standard" complex cells show this behaviour (see also Gilbert, 1977). It was, however, apparent that cells of both the "special" and "standard" populations unresponsive to bar

flash are more broadly tuned than cells responsive to bar flash suggesting a functional difference.

Some distinctions between "standard" and "special" complex tuning characteristics were, however, noticeable. While both groups showed a shift in the peak of spot tuning compared to bar tuning, the shift was more pronounced for "special" complex cells. Also, as a group, "standard" complex cells were more sharply tuned for a moving bar than "special" complex cells. Harvey (1980) has commented on the inverse relationship between orientation and direction selectivity. There was also some indication of class-specific differences in directional bias between "standard" and "special" complex cells; "standard" complex cells direction biased for bar were directionally selective for spot but "special" complex cells direction biased for bar could also be biased for spot. Data are too limited to draw firm conclusions. Differences in breadth of tuning for spot and texture-field tuning were clearly class-specific. It remains an unanswered question the extent to which differences amongst the complex cell population are obscured by a lack of information about laminar distribution of recorded units.

The finding of a cell with bimodal tuning for a moving contrast bar is interesting in suggesting a greater diversity of complex cells' tuning characteristics and receptive field organization than has previously been described for striate cortex. Cells with more than one preferred orientation have been reported in extrastriate cortex by Hubel and Wiesel (1965). Hubel and Wiesel (1965) described "higher order" hypercomplex cells in area 19, the distinguishing

characteristic of which was the property of responding to a moving contrast bar at two different, orthogonal orientations. Such neurones were exclusive to area 19, typically in "columns" which contained complex and "lower order" hypercomplex cells, some of which responded to one of the two orientations to which the "higher order" hypercomplex cell would respond, other members of the column responding to the other orientation (Hubel and Wiesel, 1965). Hubel and Wiesel (1965) suggested the construction of the "higher order" hypercomplex cell receptive field by input from complex and "lower order" hypercomplex cells of the same column with each of the two preferred orientations deriving from the preferred orientations of the two populations of complex and "lower order" hypercomplex cells. "Higher order" hypercomplex cells had receptive fields close to the representation of the area centralis.

The unit described in the present study had peaks in the moving bar tuning curve separated by 40 deg. Stability of the bimodal tuning for a moving contrast bar over a period of two hours would argue against an artefactual basis for the tuning curve. While caution should be exercised in putting too much weight on the observations from one unit, recently other such units have been recorded (P. Hammond; J. Crook; personal communications) giving support to the existence of a group of complex cells with bimodal tuning for a moving bar.

A characterization of the tuning properties of these neurones would be a precondition for an understanding of the receptive field structure underlying their stimulus selectivity

and functional role. A primary question is whether the bimodality is related to the bimodality in tuning for a moving texture-field seen for some complex cells. The unit recorded in the present study would argue against this; it was unimodal in texture field tuning. Hubel and Wiesel's (1965) suggestion of formation of "higher order" hypercomplex cells' receptive field structure from excitatory input from two populations of cells of the same "column" with orthogonal preferred orientations is clearly an inappropriate basis for explaining bimodality of bar tuning in area 17. How such neurones in area 17 might have their receptive fields constructed is unclear. Whether such neurones "cluster" in distribution as was the case for Hubel and Wiesel's (1965) population of higher order hypercomplex cells in area 19 would be interesting to investigate. The point emphasised at this stage is that of a greater diversity of tuning properties of complex cells than previously suggested and that such neurones exist in striate cortex and are not exclusive to extrastriate cortex.

5.5 The Role of the Complex Cell in Visual Analysis

1. The Representation of Form

Approaches to the representation of form are broadly divided between those models which posit single cell modes of representation and those which suggest representation in the responses of a population of neurones; these quite different approaches are labelled "feature extraction" and "population coding" models respectively. The latter includes Fourier models. Hubel and Wiesel's (1962, 1963) model falls into the

category of a feature extraction model. The feature-extraction
models have their origin in studies of the stimulus specificity
shown by retinal ganglion cells of frog and rabbit (Barlow
1953; Lettvin, Maturana, McCulloch and Pitts, 1959, Lettvin,
1961; Maturana, Lettvin, McCulloch and Pitts, 1960; Barlow,
1964). These early studies revealed cells with highly specific
stimulus requirements suggesting a feature extraction role for
the single cell. The coding operations which a cell performs
would be delineated by reference to the feature of the visual
scene to which the single cell seems optimally sensitive. The
role of the single cell is to extract that feature from the
visual environment.

Between trigger feature and receptive field structure a
relationship of key to lock is implied. Feature-extraction
models require that the firing of the single cell signifies to
the brain the occurrence of a particular stimulus in a certain
part of the visual field. The formation of a "Gestalt" from
elementary features requires a hierarchical organization of
neurones with convergence at each level with higher order
neurones whose firing represents a stimulus symbolized by a
word (Creutzfeldt and Nothdurft, 1978). Feature extraction
implies that perceptions are caused by the activity of a small
number of neurones selected from a very large population of
predominantly silent cells (Barlow, 1972).

Feature-extraction models have been held to be logically
and empirically untenable (see Uttal, 1971; Szentagothai and
Arbib, 1974; Creutzfeldt, 1977, 1978 for reviews). A central
argument against the feature extraction approach is that the

single cell cannot signify the presence of a stimulus since few, if any, neurones increase their firing rate as a function of only one stimulus parameter (Erikson, 1968; Uttal, 1971; Poggio, 1972; Hoeppner, 1974; Bartlett and Doty, 1974; Hammond and MacKay, 1977). Even for one stimulus parameter cortical neurones are often broadly tuned so that widely separated values of the presumed trigger feature produce equivalent discharge rates (Erikson, 1968; 1974).

Hubel and Wiesel (1962, 1963) proposed a role for the single cell in contour analysis. In their variant of the feature extraction model the striate cortex was divided into functional units or "columns" within which serial analysis was undertaken by the simple, complex, hypercomplex chain. Serial analysis by such a hierarchical chain, with convergence at each stage, is theoretically unsound and contradicted by known patterns of intracortical connections. Creutzfeldt and Nothdurft (1978) commented that convergence from simple to complex to hypercomplex cells would lead to a loss of information from one level to the next without gaining unequivocal and sufficiently exact information on the feature that is supposed to be represented at the next level. Patterns of connectivity between simple and complex cells are not constrained by a serial chain (Hoffmann and Stone, 1971; Stone, 1972; Stone and Dreher, 1973; Toyama, Maekawa and Takeda, 1973, Toyama, Kimura, Shida and Takeda, 1977; Movshon, 1975; Hammond and MacKay, 1977). In striate cortex, there is no hypercomplex cell stage (Dreher, 1972; Camarda and Rizzolatti, 1976; Wilson and Sherman, 1976; Hammond and Andrews, 1978a, b; Leventhal and Hirsch, 1978), though cells

with complex tuning properties have been described in area 18 and 19 of the cat (Hubel and Wiesel, 1965; Hammond and Andrews, 1978b) and in the inferotemporal cortex of monkey (Gross, Rocho-Miranda and Bender, 1972). Evidence for papal neurones (Barlow, 1972) remains, however, scant.

A question of importance for the "orientation detector" model is in the synthesis of elements of contour to represent shapes. Creutzfeldt and Nothdurft (1978) have raised objections to Hubel and Wiesel's (1962, 1963) model if it is assumed that the synthesis occurs in striate cortex and that the cortical representation is an affine transformation of the visual scene. Creutzfeldt and Nothdurft (1978) suggested that the necessary, but also sufficient condition for synthesis is that the responses elicited by the successive points of a line should be represented in an orderly sequence in the cortical map of the visual field i.e. the representation of the visual field, at the cortical level, should be an equivalent transformation of the real world. Splitting up of the continuous representation of contours in the cortex because of clustering of cells with similar orientations into columns impedes formation of a Gestalt. A counter argument to this criticism would be either to assume that continuity of line elements to form shapes is produced by specific patterns of connectivity within the striate cortex or that the synthesis of elements occurs at a stage beyond the striate cortex. However, when the shape of an object is defined by a texture contour the problem of continuity of contour elements is particularly acute (see Caelli, Preston and Howell, 1978).

The alternative to the representation of form by a hierarchical process of feature extraction is some form of population coding. Population coding does not necessarily preclude form representation by contour analysis. Positing a model of population coding, however, raises the question of the roles performed by simple and complex cells in the population response.

(11) The Role of the Complex Cell in Visual Analysis

It has been suggested that simple and complex cells perform parallel roles in visual analysis by virtue of differential input from the lateral geniculate nucleus (Hoffmann and Stone, 1971; Stone, 1972). The retino-geniculate pathway has been conceived as comprising distinct channels beginning with the major groupings of ganglion cells which subserve distinct functions (Rowe and Stone, 1980). Separate channels mediating information about form or motion have been suggested (Tolhurst, 1973; Kulikowski and Tolhurst, 1973). Segregation of parallel pathways at the geniculo-cortical synapse could determine that simple and complex cells receive and process different aspects of the visual image. If X and Y pathways were to be equated with "form" and "motion" channels (Tolhurst, 1973; Kulikowski and Tolhurst, 1973), and if the X and Y streams were to segregate at the geniculo-cortical synapse with X input to simple cells and Y input to complex cells (Hoffmann and Stone, 1971; Stone, 1972), this might suggest that simple and complex cells constitute form and motion analysing systems respectively. Psychophysical evidence for form and motion channels, the

equation of these with X and Y pathways and the association of simple and complex cells with form and motion analysing systems is therefore evaluated.

Psychophysical evidence for separate "form" and "motion" channels is substantial. For example, Tulunay-Keesey (1969) reported that flashing or flickering a bar-shaped stimulus pattern prolonged its visibility but that, at flicker frequencies 5-30 Hz perception of the flicker of the stimulus persists after the perception of its shape is lost. Tolhurst (1973) confirmed Robson's (1966) observation that flicker increases the visibility of coarse but not fine grating stimuli and Blakemore and Campbell's (1969) observation of a lowest adaptable spatial frequency channel. But, additionally, Tolhurst (1973) reported that when the adapting grating was moving instead of stationary, channels selective for frequencies much coarser than the coarsest channels detected with stationary gratings were evident. Kulikowski (1971) reported that the psychophysical threshold for the perception of flickering gratings depends on whether they are switched on or off or counterphased and that the threshold for counterphase was half that for on-off flicker at low spatial frequency but fine gratings' threshold for counterphase and on-off modulation did not differ. Interpretation of some of these experiments has been questioned (see Macleod, 1978 for review).

Behavioural studies with the cat have produced evidence consistent with human data in suggesting separate form and motion channels (Blake and Camisa, 1977). Identification of form and motion channels with cat X and Y fibre systems was

suggested by Tolhurst's studies (1973). Tolhurst (1973) noted that 'movement' channels were very sensitive to low spatial frequencies (<3 cycles/deg.) and 'pattern' channels to high spatial frequencies (>3 cycles/deg.), properties similar to Y and X fibres respectively.

The picture is more complex. Kulikowski and Tolhurst (1973) have shown that pattern detection is mediated by the X-like system at high spatial frequencies and by the Y-like system at low frequencies. At intermediate frequencies, both systems are likely to contribute to this function. Lennie (1980) reported that when the temporal contrast sensitivities of X and Y ganglion cells, in cat, are measured under conditions in which shape and motion channels are demonstrated psychophysically, Y cells are no less sensitive than X cells to stimuli at low temporal frequency. X/Y pathways do not segregate into parallel and independent simple/complex streams at the geniculo-cortical synapse (Ikeda and Wright, 1975; Singer, Tretter and Cynader, 1975; Movshon, Thompson and Tolhurst, 1978a, b, c; Lee, Heggelund, Hulme and Creutzfeldt, 1977; Bullier and Henry, 1979a, b, c; Tanaka, 1983). Simple and complex cells cannot be equated with 'form' and 'motion' processing systems. The existence of a third retino-striate pathway, for W cells, provides a further complication in understanding information transfer via parallel pathways to the striate cortex.

Though distinct roles for simple and complex cells cannot be established as a product of differential input from the lateral geniculate nucleus, a number of properties do, however,

suggest distinct roles for simple and complex cells in visual analysis: the sharper tuning of simple compared with complex cells (Henry, Dreher and Bishop, 1974; Watkins and Berkley, 1974; Albus, 1975; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978; DeValois, Yund and Hepler, 1982); the greater symmetry of tuning of simple compared with complex cells (Henry, Dreher and Bishop, 1974; Hammond and Andrews, 1978b); constancy of tuning for simple cells, but increased breadth of tuning for complex cells with eccentricity (Gilbert, 1977; Leventhal and Hirsch, 1978; Watkins and Sherman, 1976); an increase in the proportion of complex cells with eccentricity (Wilson and Sherman, 1976). Moreover, preferred velocity and velocity cut-off are typically higher for complex than simple cells (Movshon, 1975; Wilson and Sherman, 1976). Simple and complex cells are differentially sensitive to texture-field motion (Hammond and Mackay, 1977 and subsequently). Complex cells produce excitatory responses during saccadic eye movements, but simple cells are inhibited (Kimura, Komatsu and Toyama, 1980). In sum, simple and complex cells are distinguished by tuning properties and function under different circumstances.

In the following analysis it is suggested that both simple and complex cells have a role in the representation of form but that the role of the complex cell is distinct from that of the simple cell. Form representation is viewed as a non-unitary mechanism and complex cells are ascribed a role in the representation of the form of moving objects. A functional interpretation is given to asymmetries of tuning for a moving bar. The central contention is that asymmetries provide not

only a pre-condition for direction-selectivity but also a compensation for distortion of form associated with stimulus movement. Consideration is also given to the fact that the form of a moving texture-bar can be seen under conditions in which cells respond only to texture <u>motion</u>. It is concluded that this result requires a role for direction-selective units in the representation of form.

Creutzfeldt and Nothdurft's (1978) investigation of the transfer properties of simple and complex cells emphasised a role for simple cells in foveal vision. These authors suggested that the (orientation-selective) simple cells could play an important role for static hold and guide functions of gaze during foveal exploration, fixation and binocular fusion as simple cells are ideally suited to localise and monitor contours. Creutzfeldt and Nothdurft (1978) noted the sensitivity of complex cells to movement of texture and contrast and to higher speeds of movement; complex cells cells become active if a contour or texture of the fixated visual environment moves relative to it. Creutzfeldt and Nothdurft (1978) therefore suggested a role for the complex cell system in representing movement relative to a still structure as it is represented by simple cells and to guide visual behaviour towards the moving object.

The role of the complex cell in monitoring the movement of a textured surface receives firm support from the work of Hammond and associates (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980, for example). Hammond and Smith (1983a, b) have demonstrated that complex, but not simple

cells, can resolve relative motion.

There is a specific problem relating to pattern recognition of moving objects which may provide a functional interpretation for the asymmetry shown in tuning for a moving bar. The interpretation derives from Fromel's (Fromel, 1977, 1980a, b) and Dinse and von Seelen's (1981a, b) analyses of problems of feature extraction in the context of studies of the superior colliculus and area 18 respectively.

Dinse and Von Seelen (1981a, b) have argued that since the (cat's) visual environment is not recognizably asymmetrical, there is no reason for implementing the recognition of stationary patterns with asymmetrical coupling of neurones. It is known that the projection of the retino-geniculate pathway onto the striate cortex is retinotopically organized (Whitteridge, 1973; Tusa, Palmer and Rosenquist, 1978). Both Fromel and Von Seelen and Dinse have argued that the conditions of pattern recognition change under conditions of stimulus movement. Fromel (1980a) has commented that symmetrical spatial coupling (as for example seen in the retina) shows distortion in the temporal domain so that pattern recognition is rendered difficult. As a product of the temporal properties of the symmetrical coupling, determination of where a moving object is located is subject to a systematic spatial error which is dependent on velocity. As velocity increases, the maximum of the output value lags behind that of the input value so that an error occurs when determining the position of a moving object.

In the same vein, Dinse and Von Seelen (1981b) stressed that in conditions of stimulus movement, "a time dependent variable must be involved in the space transformations necessary for pattern recognition due to the time lag at synapses. Due to causality, the time domain is in principle asymmetrical. So, when the pattern moves, there is always dispersion in 2-dimensional networks i.e. the patterns are distorted in a way dependent on their velocity and appear to the analysing system to be positioned wrongly with reference to the external co-ordinate system."

Potentially, distortion of pattern associated with its movement might be overcome by a central computation from simultaneously measuring the spatial error in localisation of a moving object or by compensating for the error. Both Fromel (1980a, b) and Dinse and Von Seelen (1981b) argue for compensation; distortion is compensated by asymmetrical coupling of neurones. One may therefore argue that the asymmetry of bar tuning of complex cells for a moving bar reflects not only the coupling determining direction selectivity but also provides compensation for distortion associated with stimulus movement. The present study provides evidence for Dinse and Von Seelen's (1981) contention that asymmetrical coupling is probably a general principle of neuronal connectivity that eliminates distortions of moving patterns and allows the direction of movement of stimuli to be coded by a neuronal network. Most important, asymmetrical coupling of neurones means that form analysis does not require a stationary image.

The results from comparison of tuning for a texture-bar with moving contrast bar and texture-field are problematical both for a hierarchical feature-extraction model and for a model invoking population coding by contour analysers; simple cells are unresponsive to moving texture-bars (Hammond and Mackay, 1977) and complex cells respond only to texture-bar motion. Perception of form, under conditions in which cells are unresponsive to contour, prescribes a role for direction-selective units in the mediation of form. That role is provided by complex cells.

Psychophysical evidence has suggested both that form representation is not mediated by a unitary mechanism and that some aspects of form analysis may be achieved by direction-selective units; separation of moving objects from one another and from a background or the reconstruction of a three dimensional object (Wallach and O'Connell, 1953; Gibson, Gibson, Smith and Flock, 1959; Julesz, 1971; Ullman, 1979). Marr and Ullman (1981) have suggested that a population of direction-selective units may be used to separate figure from ground by instantaneous measurements of the motions of elements in the visual field. Phenomenologically, the shape of an object would arise from discontinuities in the motion field as defined by the population of direction-selective units. The theoretical perspective is neatly summarized in the following quotation from Marr and Ullman, 1981.

"If the complex velocity field is given (i.e. speed and duration at each location) boundaries will be indicated by discontinuities in this field. This is because the motion of a

rigid object is locally continuous in space and time. The
continuity is preserved by the imagery process, and gives rise
to what might be called the principle of continuous flow,
according to which the velocity field of motion within the
range of rigid objects varies continuously everywhere except at
self-occluding boundaries. Since the motions of unconnected
objects are unrelated, the velocity field will often be
discontinuous at object boundaries. Conversely, lines of
discontinuity are reliable evidence of an object boundary."

In conclusion, there is an interesting paradox presented
by the work reported in this thesis; evaluation of orientation
tuning of complex cells has revealed much about the mechanism
determining direction selectivity but consideration of the
complex cell's direction selectivity has revealed even more
about the role of the complex cell in the representation of
form.

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DIRECTIONAL AND ORIENTATIONAL TUNING IN THE STRIATE CORTEX
OF THE CAT FOR CONTRAST AND TEXTURED STIMULI.

AUTHOR TIGWELL. D. A

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