SPATIAL, TEMPORAL AND CHROMATIC PROPERTIES OF HUMAN SCALP-RECORDED POTENTIALS EVOKED BY PATTERNED VISUAL STIMULI

by

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Abstract

A series of experiments are reported in which the spatial, temporal and chromatic properties of the initial components CI and CII of the transient pattern-onset VEP, of predicted striate and extrastriate origin, are examined. Where relevant the response properties of these components are compared with those of single units in the mammalian visual system and with psychophysical data in man obtained under comparable stimulus paradigms.

In chapters 3 to 5 the time course of temporal summation of CI and CII for single time varying stimuli of variable contrast are examined. The time course of temporal summation and the interval for complete temporal resolution of CI for brief discrete pairs of patterned stimuli of the same or opposite polarity has also been studied, and the data related to psychophysical phenomena. The results of the experiments in chapter 6 suggest that high frequency VEPs elicited by patterned stimuli are generated by the same region of visual cortex as that of the CI component of the transient pattern-onset VEP.

The experiments of chapter 7 to 9 were designed to seek electrophysiological correlates of the psychophysically identified 'sustained' and 'transient' visual processing channels, and of various types of pattern masking phenomena which have been postualted to be the result of neuronal interactions between these channels.

In chapter 10 an adaptation paradigm is used in conjunction with grating and regular dot patterns, to seek electrophysiological evidence for 'length' and 'non-length' selective channels which have been postulated on the basis of psychophysical data.

The results of experiments reported in chapter 11 show that both CI and CII are sensitive to patterns of isoluminant colour contrast; a finding consistent with single unit data from monkey, and suggesting that many cells within the human visual cortex signal both luminance and colour contrast. The scalp distribution of these colour and luminance contrast VEPs are compared in detail in chapter 12.

In chapter 13 further stimulus specificities of the CI component are investigated.

CONTENTS

Chapter 1

Introduction

Visual perception can be studied by two main techniques; psychophysics and electrophysiology. The former has in general been reserved for studies of the human visual system, because of the involvement of behavioural responses of some kind. Physiological studies of cellular function are reserved for lower mammals because it is necessary to undertake surgery (see however Marg, 1973). While both approaches provide us with data unique and valid in their own right, particular interest has been devoted to the possible relationship between the two. Unfortunately the nature of the physiological techniques does not allow a direct investigation of this relationship in man.

However in the human subject a more general level of physiological activity can be sampled by recording the electrical activity from the surface of the scalp, and in particular from regions overlying the occipital lobe. It has been hoped that this 'visually evoked activity' (VEP) can be used as a 'linking technique' (Campbell & Maffei, 1970) by which investigators may determine the anatomical locus and properties of those mechanisms that underlie visual perception. The purpose of this study is to examine the stimulus specificities of VEP components of separate cortical origin, which are elicited by the appearance of patterns of spatial contrast, with a view to revealing the types of processing undertaken there.

In the following sections some limited background information on the known properties of those VEP components studied in this thesis will be given and, since our understanding of them and the inferences drawn from them are dependent on making certain assumptions about the similarity in the organisation of human visual system and that of cat and monkey (from which most of the available physiological data is derived), a section will be devoted to describing some of the relevant physiological data.

1-1:- Types of VEPs

There are a number of ways in which visual evoked potentials can

be elicited and analysed, but all can be divided into two categories based on the nature of the temporal stimulation, and classified as either 'Steady State' or 'Transient' (see for example Regan,1972). These main types can be further sub-divided on the basis of the stimulus used to evoke them, for example, luminance EPs produced by an overall change in the mean luminance of a structureless field, as compared to patterned flash VEPs which are evoked by an overall change in mean luminance concomitant with the appearance of spatial contrast. These forms of stimulation produce VEPs different in turn from those elicited by pattern appearance in the absence of any change in mean luminance, the so called pattern-onset VEP. A detailed review of the methods of recording and eliciting VEPs can be found in Spekreijse et al (1977).

The so called steady state VEPs derive their name from the fact that they are recorded when the 'brain' is assumed to have 'settled down' to a steady dynamic state produced by repetitive stimulation. The VEP thus recorded takes the form of a sine wave, whose fundamental frequency is similar to that of the stimulus repetition rate. Steady state EPs have been used by Regan (1972) and Estevez (1975) to plot the spectral sensitivity of the human cone mechanisms, the results obtained being similar to that reported by more classical psychophysical techniques. A review of steady state studies can be found in Regan (1972; 1981).

Whilst steady state VEPs allow a relatively quick and easy way of recording the electrical activity of the brain they suffer from the distinct disadvantage that it is difficult to localise the sources of this activity, to date no attempt has been made to do so. They provide very limited information regarding underlying physiological processes, since the stimulus paradigm employed is, by its very nature, restricted to a limited set of variables.

Transient VEPs are produced when a stimulus is presented at a relatively slow repetition rate so that the system can return to a 'steady' resting level before being further excited. The resultant VEP, recorded by time locking the signal averager to either the onset of the stimulus, or some other suitably stable reference point, is then enhanced relative to the background electrical activity of the brain, (assumed to be 'noise'), by a process of averaging over 'N' stimulus presentations. The waveform is then analysed in terms of its various component peaks, of differing latency, amplitude and polarity (see

Regan,1972). Although the process of averaging is lengthy, because of the necessity of allowing the system to return to a resting level, transient VEPs have the distinct advantage of containing significantly more information regarding the latency and intensity of cortical events; indeed it is because of this that the constituent peaks are assumed to reflect stimulus induced activity within differing regions of visual cortex. By undertaking detailed studies of the scalp topography of this activity as a function of the retinal location of the stimulus, it is possible to predict specific sites of origin for the underlying generators.

1.2:- Component Analysis

A number of models have been proposed to account for the distribution and properties of the transient VEP. Here, only those evoked by patterned stimuli presented under isoluminant conditions will be discussed; i.e., those in which a contrast pattern is presented without an accompanying change in mean overall luminance. Specifically the models of Jeffreys & Axford (1972a,b) and Halliday & Michael (1970) will be considered. The model of Lesevre & Joseph (1979) is based on patterned flash stimulation, and as no attempt was made to decompose the waveform into components which were pattern, as opposed to luminance dependent, it will not be reviewed.

Detailed studies by Holmes (1945) and Brindley & Lewin (1968) on man, have established the visual field representations within the striate cortex. Comparable data for the extrastriate areas are not available, but if a similar organisation to that which exists in monkey is assumed, a reasonably coherent model of visual field representations for man can be produced. The study of human VEP is complicated however by the fact there are a wide range of individual variations in the actual position of the visual cortex with respect to the overlying scalp (Polyak,1957). The human cortex as a whole has a great many more sulci and gyri than that of lower primates, and this further complicates what must, by its very nature, be an extremely complex. picture.

The most complete attempt to predict and account for the source locus of pattern-onset VEP components has been that of Jeffreys & Axford (1972a,b). Early studies had shown that the typical waveform profile elicited by luminance modulation was triphasic. Pattern-onset

Figure 1.1

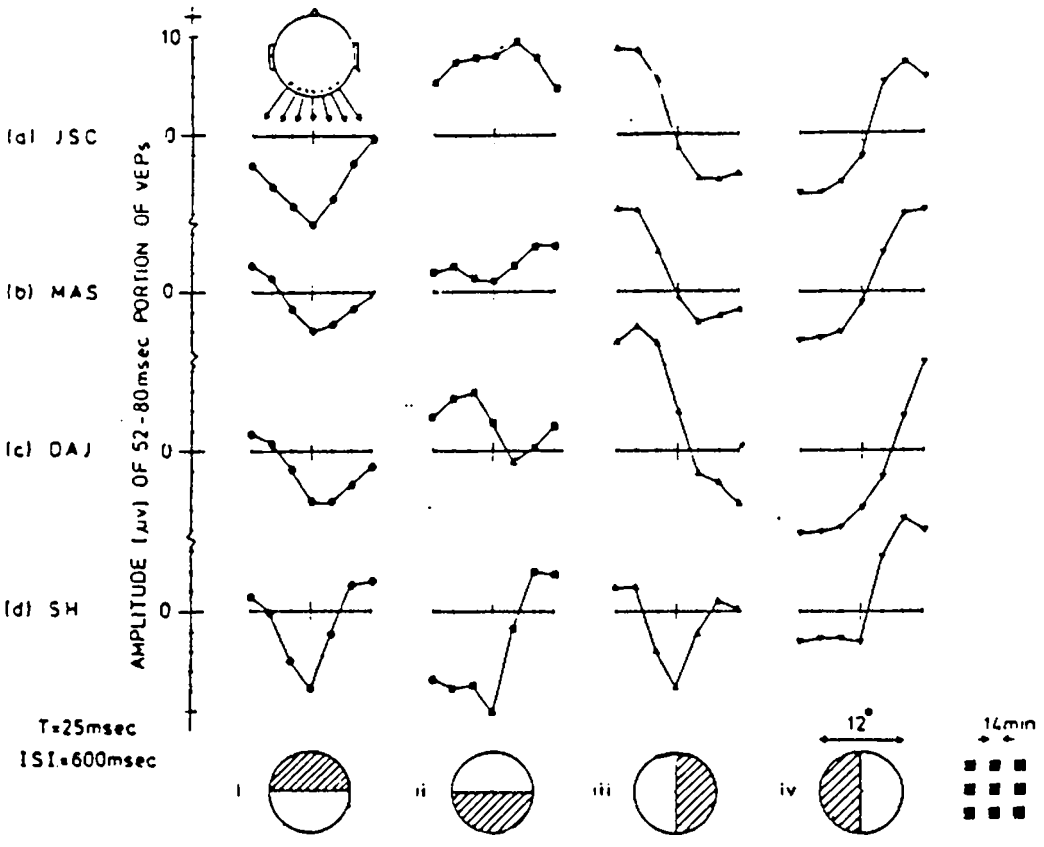
A:- Midline distribution for three further subjects. For subject S.H. upper field stimulation does not produce polarity reversal of the 85-113 msec latency sample. Such an uncharacteristic distribution might be explained if for this subject the posterior extremity of the calcarine fissure is some distance above the occipital pole, so that a greater portion of the extrastriate cortex representing the upper half-field lies on the upper surface of the lobe.

B:- Predicted potential distributions of activity along the midline at surface of volume conducting sphere due to single dipole (a) perpendicular and (b) parallel to the surface. Dipole (b) is located at the estimated position of the upper field representation within extrastriate cortex, position (a) would be consistent with the estimated location of the lower field representation.

C:- Distribution of activity for one subject from a longitudinal midline array of electrodes with upper and lower field stimulation. The latency of activity is between 90-113 msec, and illustrates the distribution of CII which is consistent with the predicted surface distribution for upper and lower field activity within extrastriate cortex.

Adapted from Jeffreys (1969) and Jeffreys & Axford (1972b).

A



Transverse amplitude distributions of the 52-80msec samples of the (i) upper, (ii) lower, (iii) right and (iv) left half-field VEPs for 4 subjects

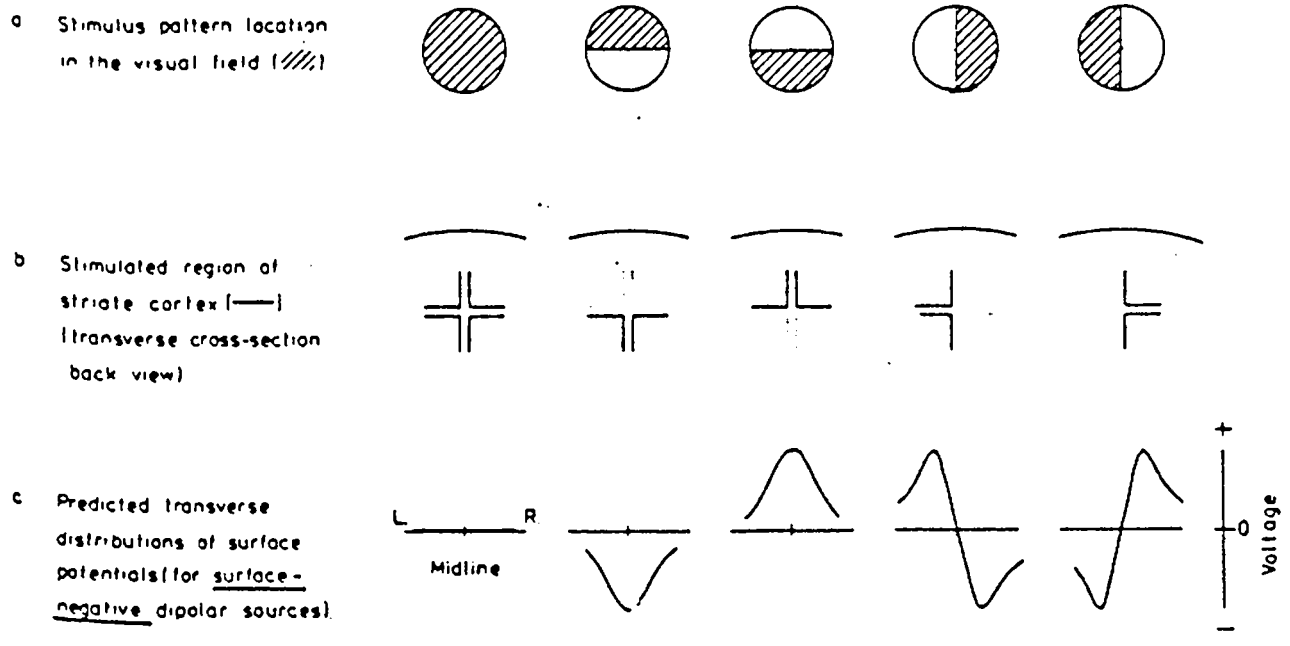


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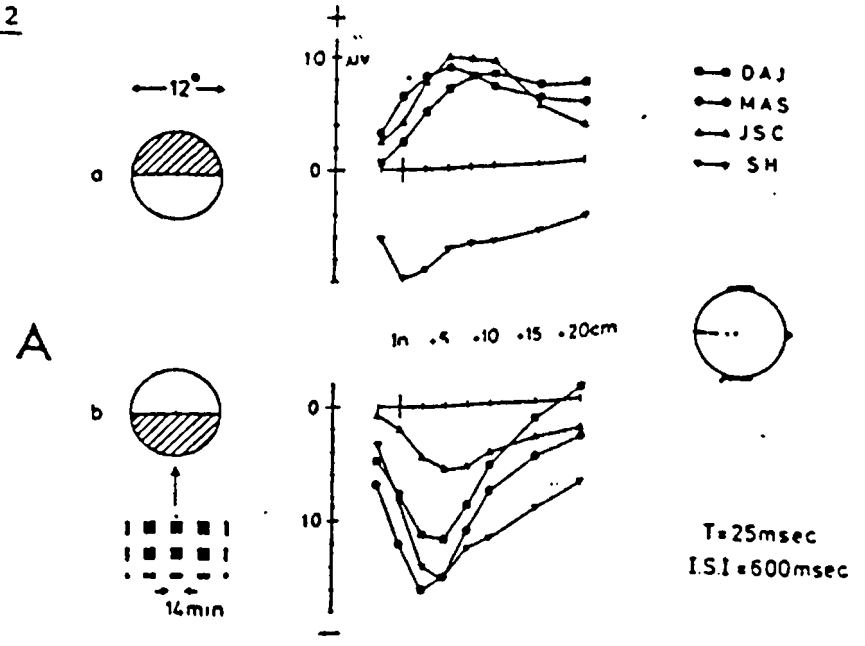
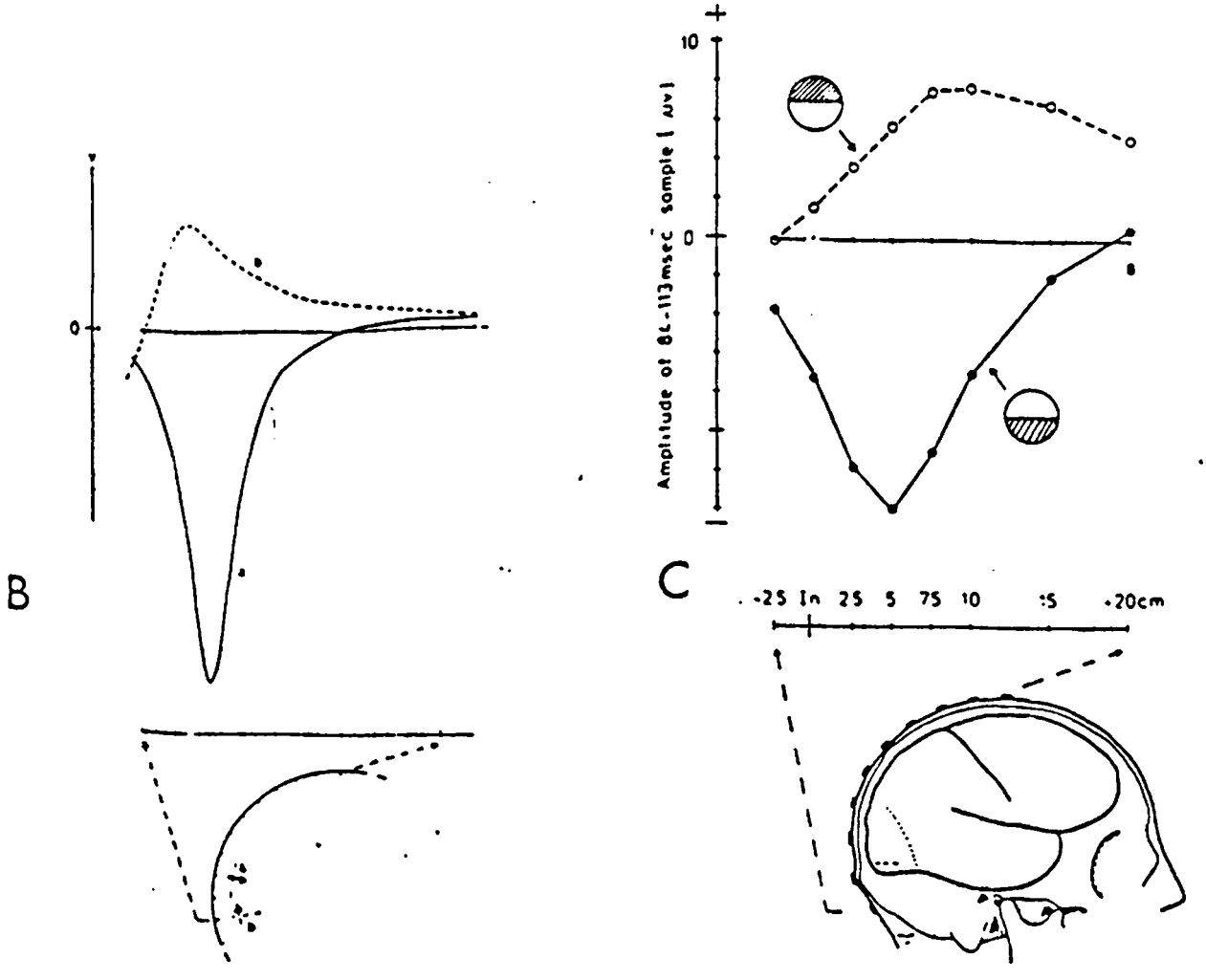
Figure 1.2



LONGITUDINAL AMPLITUDE DISTRIBUTIONS OF THE 84-113 msec SAMPLES OF (a) UPPER AND (b) LOWER HALF-FIELD VEPs FOR 4 SUBJECTS



Surface potential distributions for single eccentric dipoles oriented perpendicular (a) and parallel (b) to the surface (Spherical volume conductor) Shaw and Rahn (1955)

Longitudinal amplitude distributions of the 84-113 msec samples of the upper (- - -) and lower (——) half-field VEPs for subject DAJ

A:- Illustrates for four subjects the transverse distributions for the 60-80 msec latency sample as a function of half field stimulation. These amplitude distributions are (except for subject S.H), consistent with the theoretical distributions for surface negative dipolar sources.

B:- (a) Pattern location

(b) Schematic cruciform representation of stimulated visual field representations within and around the calcarine fissure

stimulation accompanied by a change in overall mean luminance (a patterned flash) will evoke a more complex polyphasic waveform. However Jeffreys (1968) has shown that those components of the waveform which are 'pattern specific' can be separated from luminance related components, (by appropriate subtraction techniques), indicating that components elicited by the appearance of spatial contrast are added to that of luminance activity, and thus presumably have a different source locus.

There appear to be three VEP components (CI,CII and CIII) specific to pattern-onset. For relatively high contrast stimuli presented at moderate to high luminance levels, the peak latencies of these components are, for CI, 75-80 msec, for CII some 90-100 msec and for CIII some 120-130 msec. These components can be shown to be generated in retinotopically organised regions of visual cortex since, unlike the non-pattern specific components which appear to accompany them, the peaks show polarity reversal for opposite half field stimulation. Characteristic of most subjects is the polarity reversal of CII for upper and lower half field stimulation and the polarity reversal of CI for left and right field stimulation (see figure 1.1 & 1.2). The polarity of non-pattern specific components appears to be independent of retinal location of the stimulus.

The initial justification for the assumption that CI and CII originate from striate and extrastriate visual cortex respectively, was based on studies of the scalp distribution of activity elicited by the independent stimulation of different regions of the visual field. In figure 1.1 the tranverse amplitude distributions of a 52-80 msec sample of the VEP waveform elicited by half stimulation has been shown for four subjects. These distributions bear a close correspondence to predicted transverse distributions of surface-negative dipolar sources from within regions of striate cortex onto which the visual field is mapped. In figure 1.2 are shown longitudinal amplitude distributions for a 84-113 msec sample elicited by upper and lower half field patterned stimulation. These distributions are in turn consistent with those predicted for surface-negative dipolar sources located within those regions of extrastriate cortex representing upper and lower half-fields.

Further studies have shown that not only do these components differ in their scalp distributions, but that they also have distinctive, stimulus specificities, suggesting differences in underlying physiological mechanisms processing visual information

Figure 1.3

A:- Illustrates for one subject the properties of the three components CI, CII and CIII of the pattern onset VEP.

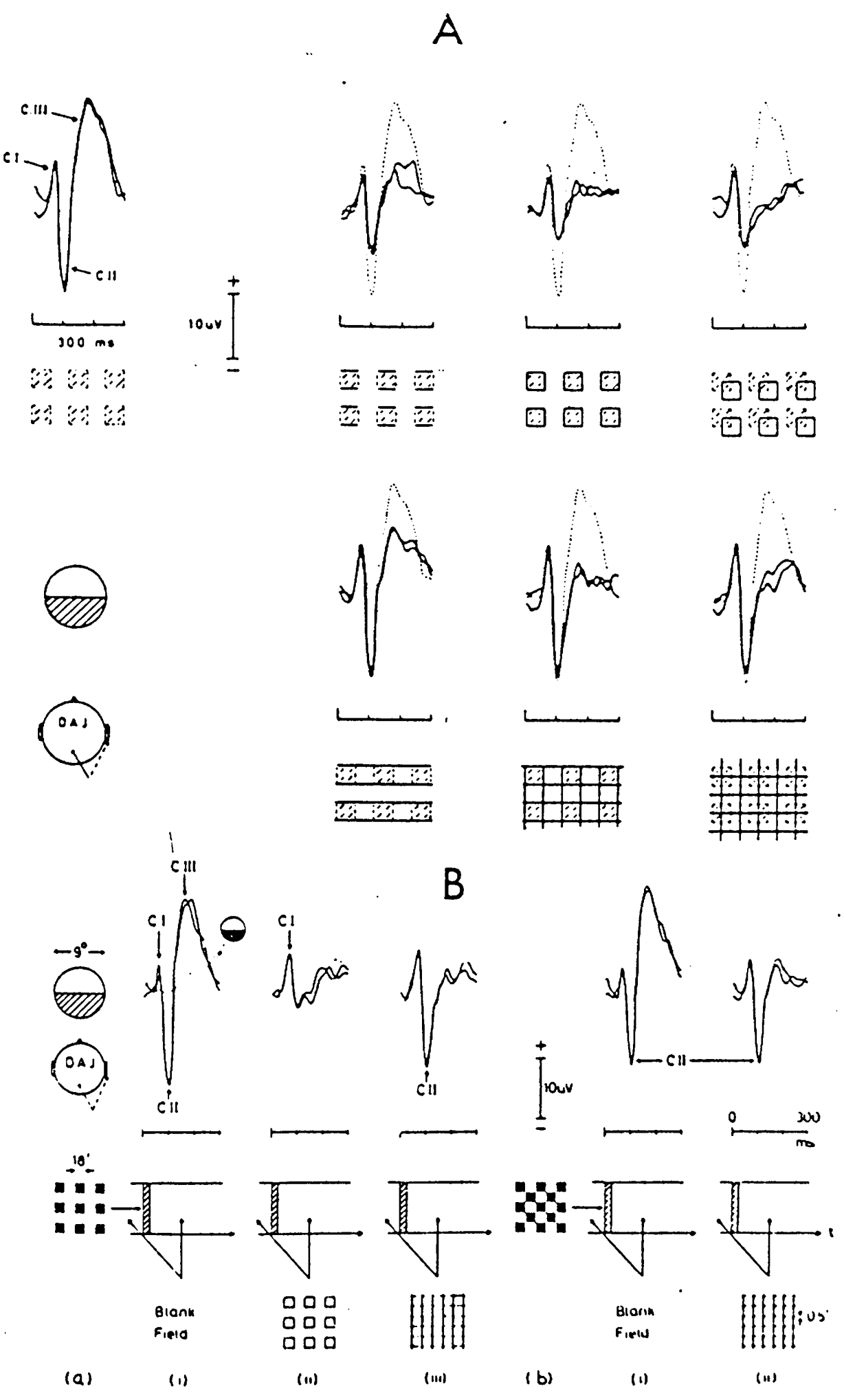
Hatched squares indicate full contrast squares in the stimulus pattern which are presented into a field containing various forms of outline elements. The form of the response obtained with the blank to pattern presentation (shown top left) are illustrated by the dotted waveforms in other cases.

In the top three rows are shown the effects of 'outlining' with discrete contoured elements of a similar size to the contrast squares.

In row 2 are illustrated the effects of outlining with continuous contours. Notice that CII is unaffected by this type of outlining, even though under these conditions there is significantly more contour, or spatial contrast within the adapting field. CIII however still shows significant attenuation.

B:- Illustrates the characteristic dependency of CII on discrete elements in the outlining effect. Notice that the outlining of checkerboards does not attenuate CII, but there is a marked reduction of CIII.

Courtesy of D.A.Jeffreys.


A
C III
C I
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300 ms
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C III
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C II
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(ii)
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within these regions of cortex. Thus, for example, Jeffreys (1977) reports that the CII component is highly contour specific. By this term is meant the fact that when stimulus patterns containing discrete, isolated elements are presented into a stationary field containing the outlines of these elements, CII and CIII are almost completely attenuated, this being the case even when the outline contours are slightly misaligned. CI under similar conditions shows only partial attenuation; approximately 50 percent (Jeffreys,1977). Outlining effects are only observed with discrete isolated elements, the outlining of checkerboards produces little component attenuation, except at low contrast levels (see Spekreijse et al,1977).

The differences in stimulus specificities of these components, confirm that they originate from different regions of visual cortex, and the characteristic scalp distribution (see figure 1.1 & 1.2), consistent with the known visual field representations, are compelling evidence in support of the Jeffreys & Axford (1972a,b) model.

One important result of Jeffreys studies has been to show that by choosing appropriate electrode positions and by stimulating a specific region of the visual field (each of these determined by undertaking a detailed study of the overall distribution of scalp activity as a function of the retinal location of the stimulus) it is possible to selectively isolate and enhance the amplitude of CI and CII relative to one another and so to study their properties in detail. This procedure is necessary because the relationship between the VEP peaks and underlying components, i.e., the separate contributions to the overall VEP from different cortical regions, is not a straightforward one, (see Jeffreys,1980).

Components overlap temporally and there is no consistent relationship between VEP 'peaks' and underlying cortical activity thus the amplitude of any single peak will depend not only on the latency and amplitude of the underlying component, but also on the relative amplitude and polarity of preceding and/or succeeding components (Jeffreys,1980).

Jeffreys & Axford's model was developed from studies of the pattern-onset VEP, Halliday & Michael (1970) have developed a comparable and, according to some, a conflicting model for the pattern-reversal VEP. The two models do not necessarily conflict with each other because of the differing modes of stimulation. Halliday & Michael (1970) identified a component of the pattern reversal response

which had a latency of 100 msec and was surface positive for the lower half field and surface negative for upper field stimulation. Because the maximum amplitude for upper and lower half field stimulation was usually recorded 5-7.5 cm above the inion, Halliday & Michael suggested that this component was of extrastriate origin.

There are problems with this model however (see Jeffreys (1977) for a detailed discussion). For example Jeffreys (1977) has questioned the evidence that polarity reversal occurs for the pattern-reversal response for either vertical or horizontal octants of upper and lower fields. Indeed he argues for a CI contribution to the reversal response with possibly some offset activity, which originates from a non-retinotopically organised region of visual cortex. (see also Estevez & Spekreijse,1975).

The Jeffreys & Axford model is given indirect support by data from studies of monkey VEP reviewed below.

1.3:- Monkey VEPs

Despite the widespread use of VEPs in man both as a research tool and as a clinical diagnostic aid, there is little evidence, other than that of surface mapping studies, indicating the specific cortical origin of the various components of the scalp recorded waveform. Animal preparations (particularly monkey) have not been used extensively enough to provide a more concrete basis for our understanding of

a:- the relationship between surface components and underlying cortical generators,

and

b:- the relationship between physiological processes (single unit properties) within those cortical regions and the specific stimulus-dependent properties of the VEP components themselves. This is doubly regrettable, both from the point of view of providing a clearer understanding of the implications to be drawn from VEP studies in man, as indicators of stimulus specific physiological activity, and from a purely theoretical perspective, in providing some clearer understanding of the much overlooked importance, of the patterns of stimulus-specific, 'spatially extensive' (Mackay,1981) activity within neuronal populations. The preoccupation of neurophysiologists with characterising and classifying receptive field properties and cortical cell types has led some to overlook this important issue (though see

Creutzfeldt & Northrofdt,1978; Mackay,1980).

The apparent disinterest in the relationship between surface and intro-cortically recorded activity is regrettable because the few studies which have been conducted on the monkey, have revealed interesting data showing neural activity, with similar latency differences between regions of visual cortex to that predicted by Jeffreys & Axford (1972) from the latency and time course of CI and CII. For example Perryman & Lindsley (1976) report that large pattern-onset responses can be recorded from the surface of monkey striate and extrastriate cortex, and further, that these potentials are not evident with unpatterned luminance stimulation. The latency of peak activity within striate cortex was reported to be 75 msec (similar to CI) and it was observed that the amplitude of the potential depended on contour density.

A second phase of activity was recorded over area 18-19. Two components were evident, the largest of which had a peak latency of 100 msec (similar to CII) and was also found to increase in amplitude with increasing contour density and contrast. The other, later component was a long duration response with a poorly defined peak latency, of between 300-350 msec; its amplitude again an increasing function of contour density. These workers also reported that single units recorded from these regions showed greater sensitivity (increased discharge amplitude) to checkerboard as opposed to grating stimulation, similar to the effect observed for the intracortical and surface VEP.

Qualitatively similar conclusions regarding the relative timing of neural activity within monkey visual cortex has been drawn by Lieb & Karmel (1974) in a study of gross activity from parafoveal, foveal striate, foveal prestriate and inferotemporal cortex. Once again pattern stimulation evoked the largest and most consistent VEPs, the amplitude of which was an increasing function of contour and contrast density within the patterned stimulus.

The latency of evoked activity within these regions of visual cortex were as follows.

1: parafoveal cortex - 75 msec
2: foveal cortex - 85 msec
3: foveal prestriate - 90 msec
4: inferotemporal cortex - 140 msec

These workers concluded that the overall distribution of gross neural activity within striate and pre-striate cortex of monkey evoked by patterned stimuli is similar in latency to that reported by Jeffreys and Axford (1972 a,b) for the initial components CI and CII of the pattern-onset potential in man.

Padmos et al (1974) have also reported experiments in which the scalp potentials of rhesus monkey were recorded. Although less relevant to the problem of the electrogenesis of the VEP this study does provide an an illustration of the difficulties of cross species comparisons. Padmos et al noted that although large pattern specific VEPs can be recorded from monkey scalp they have, apparently, different properties to those found in man, in that there appeared to be only one major component with a polarity dependent on the location of the patterned stimulus. It is clear from the anatomy that most of the monkey cortex exposed at the undersurface of the scalp represents the striate visual area, the extrastriate regions are buried deep within cortical tissue and unlikely to produce much activity recordable at the scalp.

It is to be hoped that future studies will attempt a more detailed investigation into the relationship and possible correlations between single unit, depth and surface recorded VEP.

1.4:- The aims of the present study

The aims of the present study are twofold. Firstly it is hoped that by examining the stimulus specificities of the components of pattern-onset VEP some understanding will be gained as to the types of information processing undertaken within the human visual cortex. Also, that by making a comparison between the the properties of these components and those reported for single units recorded under similar conditions, the relationship between scalp recorded activity and underlying physiological processing will be revealed.

Secondly, this study will attempt to use the VEP as a means to test directly, in the human subject, the physiological predictions of certain models of psychophysical phenomena.

Thus in chapter 3 a series of experiments are described which examine the applicability of the contrast equivalent of Bloch's law to the CI and CII components. The properties are compared to those

reported psychophysically and at the single unit level.

In chapters 4 & 5 the temporal properties of CI are further examined, in this case with brief discrete pairs of patterned stimuli of either the same or opposite contrast polarity. The time course of temporal summation and the limit of temporal resolution are then compared with psyhcophysical and single unit data, and a relationship between the three types of data is suggested.

The values of limiting resolution obtained in chapter 4, for brief discrete pairs, is compared in chapter 6 to values obtained for a continuous series of patterned stimuli. Experiments were conducted to examine the retinal location dependency of these steady state pattern VEPs and it will be argued that their generators are isomorphic with those of CI. The increased temporal resolution observed for a patterned flicker train, as compared to a brief discrete pair, is shown to be the result of a non-linearity within the visual system.

In chapter 7 a series of experiments will be reported which will examine the proposition that the human visual system is composed of two distinct processing channels, one with a long reponse latency and optimally stimulated by high spatial frequencies, (the 'sustained' system), and the other with a shorter response latency and optimally stimulated by low spatial frequencies, (the 'transient' system). These two channels have been postulated to be the functional correlates of the 'X' and 'Y' cell system, the physiological properties of which have been reviewed in section 1.6.

The experiments reported in chapters 8 & 9 will examine further spatio temporal phenomena related to visual pattern masking. The electrophysiological functions obtained under these conditions are then compared to those observed psychophysically.

In chapter 10 an adaptation paradigm, similar to that used by Smith & Jeffreys (1978) is employed to seek electrophysiological correlates of psychophysically identified threshold elevation phenomena associated with dot and grating stimuli.

In chapter 11 the colour specificity of the CI and CII components will be studied, and in chapter 12 a series of experiments will be described which have attempted to determine the existence of colour contrast specific components. The results of these experiments suggest that, as with the monkey, the human visual cortex contains many cells equally responsive to both luminance and colour contrast.

Chapter 13 will describe a series of experiments which will examine the stimulus specificities, and the effects of background luminance on the latency and amplitude of the CI component.

The interpretation of the results of these experiments will depend on making certain assumptions and comparisons with regard to physiological studies of single cells within the cat and monkey visual system. Indeed it is partly the aim of this study to attempt to make and justify this step. Thus in the following section a brief review of the known functional physiology of the mammalian visual system will be undertaken.

1.5:- Functional organisation of the visual system

The aim of this section is to give a brief review of recent physiological studies of cells in the visual system of cat and monkey. More comprehensive accounts can be found in excellent papers by Zeki (1978a), Van Essen (1980), Rodieck (1979), Leventhal (1979), Stone & Dreher (1981).

It is tacitly assumed that VEPs recorded from the human scalp reflect, in some way the underlying physiological processing of visual stimuli. It is further assumed that certain types of stimuli and stimulus paradigms produce specific effects on VEP components which might reasonably be explained by the properties of single cells within the visual cortex. Thus, for example orientation specific adaptation of VEP components have been assumed to show the existence in human visual cortex of orientation specific cells (Blakemore & Campbell,1969) (see section 1.4) and the percentage of response attenuation of CI has been interpreted as revealing that approximately 50 % of units within the human striate cortex are monocularly driven (Smith & Jeffreys,1980). The former of these effects has for example been explained in terms of simple cell physiology. The receptive fields of simple cells found in the visual cortex of the cat and monkey are elongated, with an excitatory centre flanked by two parallel inhibitory side bands, (Hubel & Wiesel,1968). As a result of this arrangement a bar, whose length is greater than that of the receptive field, moved orthogonally to the excitatory centre and thus simultaneously crossing the excitatory centre and inhibitory surround, will be ineffective in driving the cell. Only stimuli moving in the preferred orientation, that is parallel to the the excitatory and inhibitory flanks, will optimally stimulate such cells. These cells are therefore orientation specific.

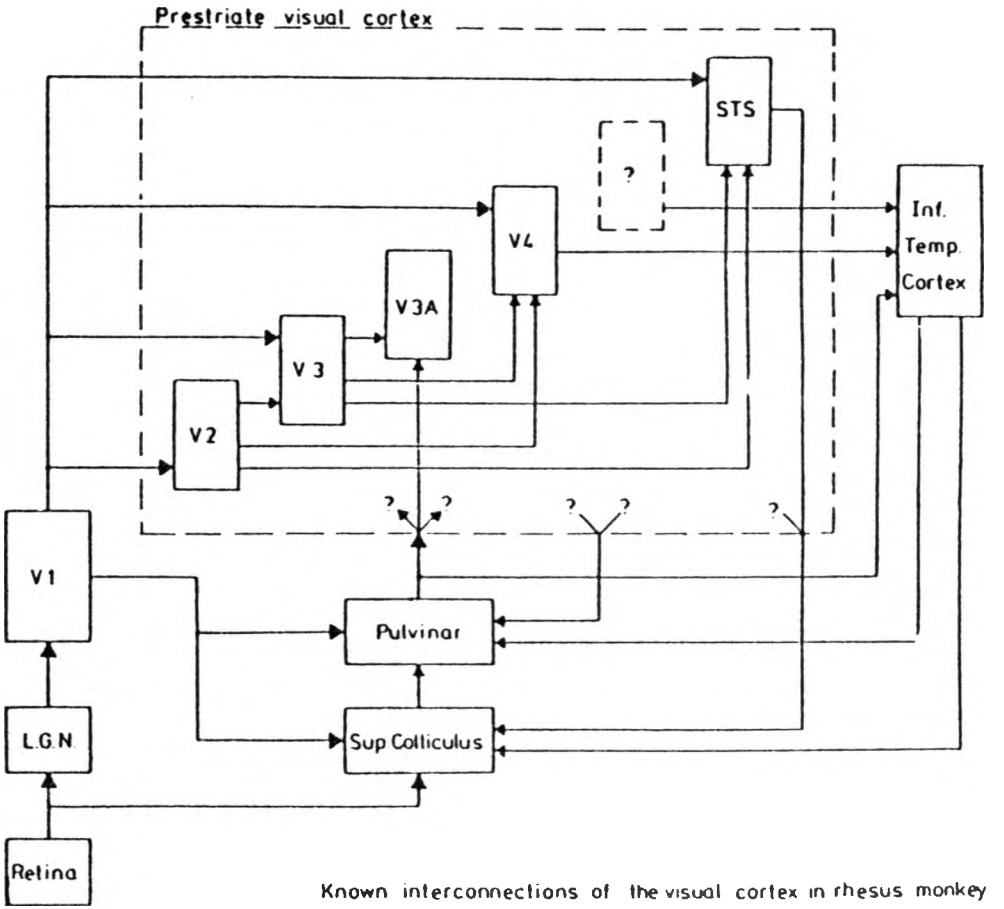
The second major group of cells identified by Hubel & Wiesel (1965; 1968) were the 'complex' class. Such cells would not be predicted to be mediating grating adaptation effects because, unlike simple cells, their receptive fields are organised in a manner such as to make them unresponsive to bar stimuli which extend outside the region of their receptive field. The 'complexity' of these cells derives from the fact that receptive fields could not be plotted with small spot stimuli and from the finding that the principle of mutual antagonism and spatial summation characteristic of simple cells appeared not to hold (see Hubel & Wiesel,1968, also Stone et al,1979).

Figure 1.4

A:- From Zeki (1978). Illustrates reported percentages of various types of cellular receptive field categories in regions of extrastriate cortex of rhesus monkey. STS = Superior Temporal Sulcus.

B:- Illustrates visual areas and known interconnections between them. Adapted form Zeki (1978a,b,c,d,) and Cowey (1979) by D.A.Jeffreys.

B



Known interconnections of the visual cortex in rhesus monkey

The receptive field organisation of complex cells led to the assumption that the afferent input to them was derived from a number of simple cells, their receptive field properties being determined by the overall balance of these inputs. It should however be noted that the classification of cells into the 'simple-complex' categories is not an unambiguous process. Indeed it is clear that cells which would be termed 'simple' by one laboratory would be classified as 'complex' by another. It is now generally agreed that the 'simple' and 'complex' classes can be sub-divided into various 'special' catergories. For example there is a 'special' complex group which show spatial summation within their receptive fields. The problem of cell classification is both a conceptual and experimenal one, and a review of the difficulties can be found in Stone et al (1979).

Simple cells appear to be the dominant cell type in layer IVc of the monkey striate cortex and since the studies suggested that this layer received most afferent input from the LGN it was assumed that simple cells were the initial stage of cortical processing. However studies of monkey visual cortex (Dow & Gouras,1970) have revealed that non-orientation specific receptive fields can be found in this layer; these cells appear to have a centre-surround organisation similar to geniculate units.

Complex cells were in greater evidence in layers above and below layer IV, which supported the assumption that they were the next or secondary stage of processing in an overall hierachical scheme of information extraction in which increasingly 'complex' features of the visual stimulus were analysed. Later studies, which examined the properties of cells on the border of area 17 and 18 and within 18 itself, revealed a further level of complexity of receptive field organisation not seen at preceding stages. These findings merely confirmed the then current view that processing within the visual cortex was undertaken on a serial basis. The discovery of these new cell types described as 'Hypercomplex' suggested that at the 'higher' visual areas the process of 'abstracting' features of visual stimuli was taken a step further. The receptive fields of this group had inhibitory end zones either at one or both ends (Hubel & Wiesel,1965; but see Dreher,1976; and Kato et al,1978), a configuration presumably mediated by a series of complex cell inputs.

Hubel & Wiesel (1965; 1973) regarded areas 17-18-19 as a chain in which an increasingly complex serial processing was undertaken in much

the same way as the simple-complex-hypercomplex chain. Appealing though this model may be, it is now considered an oversimplification and there is much data which it cannot accommodate. For example there is now conclusive evidence showing wide species differences in the terminal site of afferent fibers from the LGN. Thus it is now known that area 18 of the cat, and probably 19 as well, receives direct afferent input from the LGN. Interestingly the type of afferent input can be segregated on the basis of the 'X' 'Y' 'W' cell classification (Leventhal,1979; Stone et al,1980; Lennie,1981). Little discussion has as yet been given to the the above classification scheme (see below), however 'Y' type cells in the retina and LGN of the cat tend to have large receptive fields and poor spatial but high temporal acuity and are thus thought to play some major role in movement perception. Because area 18 in cat receives a high 'Y', and low 'X' fiber input it was suggested that it may from part of a movement processing area (see Movshon & Tolhurst,1978). Area 17 on the other hand receives a predominantly 'X' fiber input (see Stone,1972; Tretter et al,1975).

A stronger case for a serial processing "stream" could perhaps be made for the monkey where geniculate fibers terminate only in the area 17. By ablating the striate cortex it is possible to show that most of the functions of area 18 in the cat remain intact (consistent with the labelling studies, Strak,1978; see also Stone et al,1979). In monkey, a similar ablation produces almost complete cessation of visually driven activity in area 18 and 19 (Schiller & Malpeli,1978) and results in a profound disturbance of visual behaviour (Weiskrantz et al,1974).

However this does not mean that extrastriate areas do not receive some input from pathways other than those which traverse striate cortex as it is known that the LGN sends afferents to other subcortical structure such as the Pulvinar and the Superior Colliculus (in the Midbrain Recticular formation), which in turn send afferents to, and indeed receive afferents from, both the striate cortex (V1), and extrastriate cortex, V2 V3 etc (Schiller & Malpeli,1978; Rezake & Benevento,1979). The importance of the pulvinar for visual processing is less well understood, although the superior colliculus is thought to have a role in the triggering and controlling of eye movements by visual information (Richmond & Wurtz,1980).

Thus far, only the input to the cortex which is inconsistent with a strictly serial model of information processing has been reviewed. Within the cortex itself there is ample evidence, at both the micro

(cellular) and macro (functional visual regions) levels, that visual information is processed in both serial and parallel channels. Afferents from the striate cortex appear to radiate, directly and/or indirectly to all extrastriate areas (Zeki, 1974; 1978a,b,c,) where specific visual features appear to be processed. In the macaque for example, studies of cellular function have revealed marked variations in receptive field types in different regions, whilst these regions themselves show variations in the extent of the visual field represented. In V1 for example the whole of the visual field is represented with the central foveal region, being mapped onto a disproportionately larger area of cortex (Cowey & Rolls, 1964). In V2 however only the central 2 to 3 degrees of the visual field appears to be represented.

Similarly, at the cellular level the non uniformity of distribution of specific cell types leads to the obvious conclusion that some form of regional specialisation exists within these various extrastriate areas, (see figure 1.4a). The clearest evidence for this is in the medial temporal sulcus where Zeki (1974) reports cells which have a strong preference for stimuli moving in a particular direction. Direction selective cells are less abundant in other visual areas of extrastriate cortex which, given the reciprocal connections between layer IVb of the striate cortex and the medial temporal sulcus (Lund et al, 1978), would suggest that the directional selectivity of cells in the latter is mediated by direct input from striate cortex.

Colour processing is a further feature which appears to be highly developed in a specific region of extrastriate cortex. Colour contrast sensitive cells abound in the foveal representation of V1 (Gouras & Kruger, 1978), they are less common in V2, still less so in V3, V3A and the medial temporal sulcus, but are found in disproportionately high numbers in V4 (Zeki, 1974, 1977, 1978a,c; Van Essen & Zeki, 1978).

Thus it would appear that extrastriate cortex can be segregated into functional areas each with a retinotopic map differing in extent and detail. The exact number of distinct visual areas is as yet not known, Zeki (1978) reports 6 for the rhesus, and up to 12 have been reported for the cat (Allman & Kass, 1977). Whether these number are realistic can be determined only by a combination of degeneration and physiological studies, yet the existence of the very complex patterns of connectivity between visual areas makes notions of simple serial processing untenable, (see figure 1.4b).

At the single unit level we know from the work of Hammond & Mackay (1977) that complex cells can be driven with stimuli to which simple cells are unresponsive.

It is thus difficult to relate specific types of psychophysical phenomena such as grating adaptation to the properties of a limited class of cells. There are too many types of cells and the patterns of connectivity between them too complex and numerous.

Thus far, this brief description of recent neurophysiological data has concentrated mainly on the visual cortex; the input from sub-cortical structures will now be considered since recent studies have emphasised the complexity of physiological processing at these levels.

1.6:- 'X', 'Y', classification

A large body of data has been accumulated which suggests that the retino-cortical pathways may be regarded as a group of parallel pathways each composed of groups or classes of cells with differing physiological and perhaps morphological characteristics. These pathways are assumed to mediate a distinctive contribution to visual information processing. All the relevant data cannot be reviewed in detail and only those features assumed to be of functional significance will be discussed, more comprehensive reviews can be found in Lennie (1981), Leventhal (1979) and Stone et al (1980). However the results of numerous psychophysical experiments have been interpreted in terms of the properties of these channels which are hypothosized to exist within the human visual system (see for example Breitmeyer & Ganz,1976; Breitmeyer et al,1981). It is necesssary therefore to give a little background information on the physiological properties of these 'channels'.

The first and clearest distinction between these types of cells was drawn by Enroth-Cugell & Robson (1966). They discovered that for some optic tract fibers there was a position within the receptive field in which a grating pattern exchanged with a blank field of the same mean luminance evoked no response, whilst for other cells no such position could be determined. The former class were called 'X' cells and the latter 'Y' cells. The 'X' and 'Y' classes were also distinguishable by their response to sinusoidal gratings that drifted

across their receptive fields; under these conditions 'X' cells responded with a discharge modulated about a steady mean level, 'Y' cells responded to most frequencies with a large increase in average discharge rate upon which modulated responses were superimposed. DeMonesterio et al (1978) report similar linear and non-linear cells in monkey.

Cleland et al (1971; 1973) have shown that cat retinal ganglion cells can be further distinguished on the basis of the time course of their reponse. Specifically, 'X' cells respond to both incremental and decremental spot stimuli with an initial discharge which then decayed gradually whereas the 'Y' cells responded with a simple transient discharge which decayed very rapidly. The former were thus termed 'sustained' cells the latter 'transient'.

A comparable classification was proposed by Gouras (1968) for monkey ganglion cells. The "tonic" cells described by him are similar in the time course of their response to the "sustained" cells in cat, whilst the "phasic" class are similar to that of the "transient". A major species difference must be noted, which is that the tonic cells in monkey have colour opponent receptive fields whilst the 'phasic' class did not. Schiller & Malpelli (1978) have made a similar classification according to which Gouras's tonic class would be similar to their colour opponent cells and the phasic class would be similar to the Broad band class (ie broad spectral sensitivity and no colour opponency). Cat 'X' and 'Y' cells have not been shown to be differentially colour sensitive.

Peiscle & Wassle (1979) have shown that at corresponding eccentricities 'Y' cells have receptive fields about 2.5 times larger than the 'X' cell and that the the latter are highly concentrated in the area centralis, whilst 'Y' cells are distributed more evenly across the field with a preponderence in the peripheral regions. In monkey, DeMonasterio & Gouras (1975) have shown that tonic colour opponent cells have smaller receptive field centers whose diameter increased little over 20 degrees around the fovea.

Conduction velocity of afferents

The 'X', 'Y' classification is a physiological one, however Peiscle & Wassel (1979) report that the classification may have some morphological correlate. It appears that the afferent fibers of 'X'

cells are small and those of the 'Y' class are large (see Stone et al (1979) for a more detailed discussion). Thus transmission time along the 'X' afferents will be longer than that for the 'Y' group (Cleland & Levick,1971; Stone & Fukuda,1974; Ikeda & Wright,1974). This feature has much impressed psychophysists because it implies that if, as is assumed, the small receptive fields of the 'X' cell type make them a likely candidate for transmitting detailed information relevant to form processing, then it suggests that this analysis will take a longer time than those features processed by 'Y' fibers.

In monkey it is reported that the antidromic conduction time (Gouras,1968) of tonic ('X'-like) cells are longer then those of phasic ('Y'-like) cells and Schiller & Malpelli (1978) and DeMonasterio (1978) report that 'X'-like cells (tonic), had longer response, (by 1.7 times), than 'Y'-like cells (phasic).

At the LGN the similarities between cat and monkey 'X' and 'Y'-like cells are less obvious. In cat, Cleland (1971) has shown that counter parts of retinal 'X' and 'Y' cells can be observed, although the cell types are not readily distinguishable in terms of laminar distribution. Indeed Singer & Bedworth (1973) have shown that 'Y' afferents can have an inhibitory influence on the slightly longer latency response of 'X' cells. There has been much debate as to the possible functional significance of these observations for the explanation of certain psychophysical phenomena (see chapter 7 and 8, also Breitmeyer & Ganz,1976).

In monkey, 'X'-like and 'Y'-like cells are less readily distinguishable and indeed the extent to which they can be appears to depend on the battery of test used to discriminate between them (see Lee et al,1980). The major distinction in this sub-cortical body of the monkey seems to be a laminar one, between parvocellular and magnocellular layer processing. In the former, the majority of cells have long response times and colour opponent properties, in the magnocellular layers, response durations are much shorter and the cells have, in general, non-opponent properties.

Projections from the LGN

The afferent fibers from the cat LGN terminate in area 17,18 and 19. In general however afferents fibers to area 18 conduct signals faster than those to area 17. In cat, 'X' fibres project to area 17 and

'Y' to area 17, 18 and 19, (Leventhal,1979). The differential termination of afferent fibers in area 17 of the cat may explain some of the observations of Hammond & MacKay (1977) who have shown a differential sensitivity of complex like and simple like cells to visual texture and bar stimuli, although it is likely that complex patterns of intercortical wiring may be involved.

Early studies had suggested that simple and complex type cells can be distinguished in terms of their 'X' and 'Y' afferent input. Ikeda & Wright (1975) distinguished two types of simple cell based on the time course of their response to the onset of grating stimuli. Transient-simple cells were responsive to low frequency gratings moving across the receptive field whilst sustained-simple cells were more readily responsive to low rates of temporal stimulation and had a preference for higher spatial frequencies. It was natural to attempt to relate these differences to some differential 'X' and 'Y' afferent input, although it appears that the distinction is less clear cut than was initially assumed (see Lennie,1980).

Complex cells have also been distinguished on the basis of their afferent input. Movshon et al (1978) suggests that complex cells are the prime recipients of 'Y' afferents in area 18 and that this may also be the case in area 17, since complex cells show non-linear spatial summation which is characteristic of 'Y' cells at lower levels.

The implications of 'X' and 'Y' afferent input to cortex has been reviewed in detail by Leventhal (1978), Stone (1979) who have suggested a revision of the now classic Hubel & Wiesel hierachical model of cell function; the existence of 'X' and 'Y' input revealing evidence of parallel processing channels. In monkey however, the geniculo-cortical fibres from both parvocellular and magnocellular layers appear to terminate only in striate cortex, although the degeneration studies of Hubel and Wiesel (1972) show that the target lamina may differ for the two groups. Magnocellular afferents terminate in layers IVca and the upper layers of IVcb, whilst the parvocellular afferents terminate in layers IVcb and V. Mitzdorf & Singer's (1979) current source density analysis of activity in monkey striate cortex has revealed that fast conducting afferents terminated in layers IVca and IV, whilst slower conducting afferents terminated mainly in IVcb and VI, suggesting a pattern of physiological activity entirely consistent with the degeneration studies. However, given the complexity of intercortical wiring every layer within striate cortex is

potentially connected to every other (Szentagothai,1969; Lund & Boothe,1975). Thus it is not known how the parvocellular and magnocellular input determine patterns of inter-laminar activity.

The above has been of necessity a brief and thus less than comprehensive review of the data relevant to the properties of the 'X' and 'Y' cell class. The 'W' class of cell has not been refered to because as yet there is little evidence to show their existence in monkey.

Chapter 2:- General Methods

In this section a general outline of the experimental techniques employed in this thesis, and of the equipment used to present the stimuli and record the VEPs, will be given. More detailed accounts of the specific stimulus paradigms will be given in experimental sections relevant to each chapter.

2.1:- Stimulation

In most of these experiments stimuli were high contrast photographic transparencies presented in a tachistoscope. However a Hewlett-Packard X-Y display was used in one short series of experiments to present gratings of variable contrast, frequency and contrast profile (further details of this equipment will be given in the relevant chapter).

The two main tachistoscopes employed in these studies were designed and constructed by other members of the department, see figure 2.1.

Tachistoscope A had four fields optically superimposed by means of half silvered mirrors. Each field consisted of an opal perspex screen to which a stimulus pattern was attached. These were illuminated from behind by three 9 inch fluorescent tubes (Osram white, 6W) which had switching times of less than 1 msec. Maximal field size was 10 degrees. Field stops inserted in the viewing hood allowed monocular viewing where desirable.

Tachistoscope B had five fields two of which were optically superimposed by means of a half silvered mirror and presented via a beam splitter to the left eye. Two further fields were presented by the same method to the right eye. The fifth field could be presented to either or both eyes, this field was also used as a reference field with suitably positioned markers to allow the exact alignment of stimulus patterns independently presented to left and right eyes. Each field consisted of an opal perspex screen illuminated from behind by two 24 inch fluorescent tubes (Phillips Trucolor 37) which had switching times of less than 1 msec. Each field was viewed at a distance of 55 cm and subtended a visual angle of 9 degrees. The switching of the tubes was controlled by bistable units usually trigged by a Devices Digitimer which had an accuracy of 0.1 msec. Four and, if necessary, eight

bistable units were available and allowed a wide range of pulse combinations. The adjustment of field luminance was achieved by variable potentiometers connected in series with the tubes of each field, neutral density filters could also be inserted and the fields accurately matched by means of a calibrated photo transistor. Luminance was measured by an SEI photometer, and unless otherwise stated, was set at 500 cdm^{-2} for tachistoscope A and 150 cdm^{-2} for tachistoscope B.

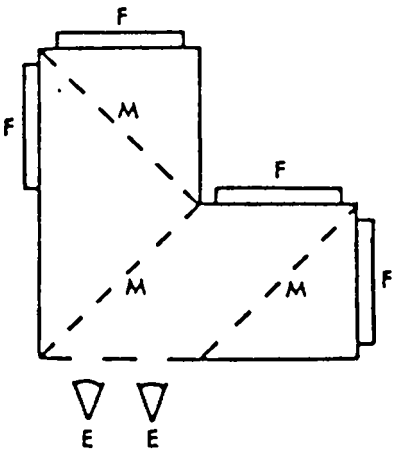
The physical contrast of the pattern stimulus could be manipulated by means of front illumination. Calibrated neutral density filters were inserted into the appropriate fields to keep the overall mean luminance constant.

A third tachistoscope (see figure 2.2) allowed the presentation of colour contrast patterns of isolated squares or square wave gratings. The method used here was similar to that employed by Regan (1973; 1975). Specifically a pattern was etched onto the surface of a half silvered mirror, (a) in figure 2.1. Coloured filters were then inserted into slots in front of the light boxes of the two fields directly behind the frontal (subjects eye view) plain of the patterned mirror. The relative luminance of these fields could then be adjusted by means of a rotatable polaroid and neutral density filters.

A third field (e) illuminated a small patternless area of adjustable colour and luminance; this was spatially contiguous with the area of contrast pattern. By adjusting the position and orientation of the moveable field stop (d) each half and quadrant of the field could be independently stimulated. Non-patterned, isoluminant stimulation was obtained by removing the patterned mirror and inserting, in its place a half silvered mirror. Overall field size was 3 degrees.

2.2:- Recording

Electrical signals were recorded from electrodes (Ag/Ag CL discs) attached to the scalp over the occipital lobe by collodion. The actual position and the electrode derivation used will be given in the relevant chapters. However, as Jeffreys (1980) has noted, before any accurate measurements can be taken of the stimulus specificities of individual VEP components care must be taken, within the limits of experimental technique, to isolate then from both partially contiguous and/or preceding and succeeding stimulus-related activity. Therefore, prior to undertaking these experiments, a surface mapping study was undertaken on each of the subjects who participated in the main series



B BEAM SPLITTER
E EYE
F STIMULUS FIELD
M HALF-SILVERED MIRROR
S SHUTTER

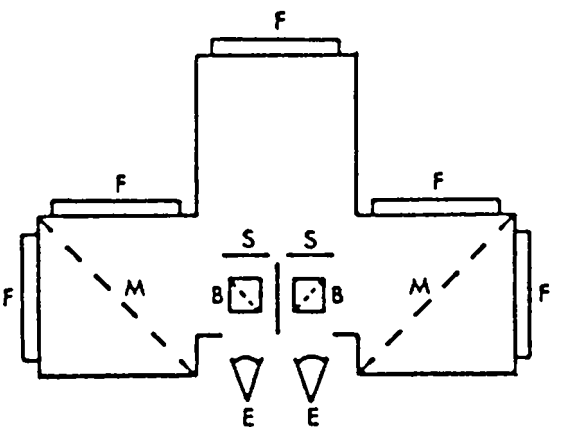


Figure 2.1

Binocular and Dichoptic Tachistoscopes.

a — Patterned mirror
b — Half silvered mirror
c — Coloured filter
d — Field stop
e — Blank field
f — Polaroid filter
g — Light boxes

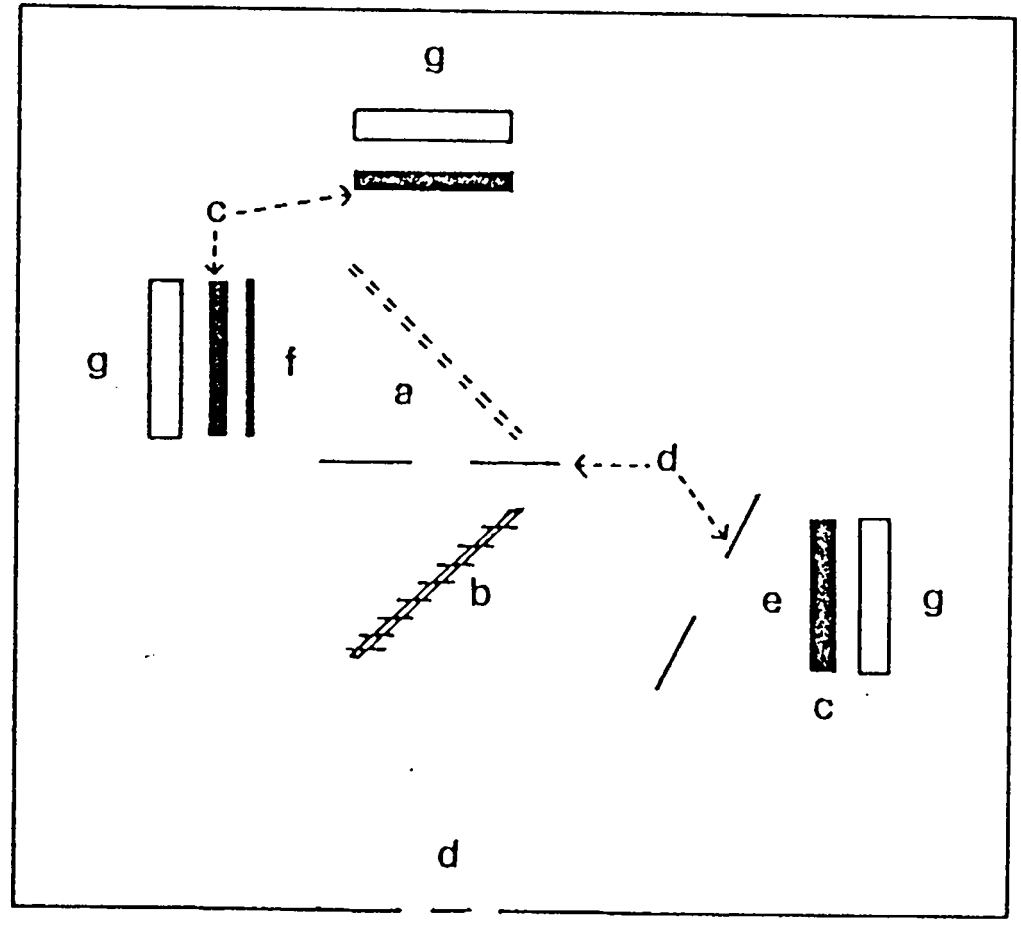


Figure 2.2

Schematic diagram of tachistoscope used to present colour contrast patterns

of experiments to determine the ideal electrode combinations and pattern location which would selectively enhance the component of interest.

For the study of the CI the stimulus was presented in the left or right half of the field and VEPs recorded bipolarly between two electrodes positioned 5cm each side of the midline, 4cm above the inion. For the study of CII the stimulus was presented into the upper or lower half of the field and VEPs recorded from a midline electrode positioned at 4cm above the inion.

The signals were amplified by a Beckman TC high-gain, multi -channel amplifier (time constant 0.3 msec, high frequency cut-off 50Hz) and recorded either on a 16 channel FM tape recorder for subsequent off-line analysis or stored on computer disc.

The FM tape recorder was used in conjunction with a Mnemotron CAT (400B four channel signal averager). Unless otherwise stated the responses were averaged over a 500 msec period commencing 100 msec prior to stimulus onset. Sampling time under these conditions was 1.25 msec; with direct computer averaging this was reduced to 1 msec. In some of these experiments the subject, usually the author, controlled the experiment using a specially constructed hand-held control box, connected in parallel with the main external control system. VEPs were monitored in the experimental chamber by a slave scope.

Usually 3 or 4 runs of 'N' sweeps were undertaken to give some indication of the consistency of the response. With the F.M. tape system, these were later re-averaged off-line to produce the final averaged waveform.

With computer averaging, a facility was incorporated into the programme which allowed for the rejection of runs in which the baseline for the period 100 msec prior to stimulus onset was contaminated by alpha activity. All accepted runs were summed sequentially, on-line, up to the value of 'N' before being stored on data disc.

2.3:- Analysis

The FM tape system, whilst having the advantage of storing all the raw data, has the distinct disadvantage that the final averaged waveform can be obtained only if the whole experiment is replayed and each of the 'N' runs for a particular stimulus condition summed on the

of experiments to determine the ideal electrode combinations and pattern location which would selectively enhance the component of interest.

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2.3:- Analysis

The FM tape system, whilst having the advantage of storing all the raw data, has the distinct disadvantage that the final averaged waveform can be obtained only if the whole experiment is replayed and each of the 'N' runs for a particular stimulus condition summed on the

CAT before being reproduced in analogue form on an X-Y plotter. This was the time consuming method employed in many of the early experiments of this thesis. The analogue waveform representing 500 msec sampling time being traced at 20 cm. In addition values of peak amplitude were obtained by digitising the points of the CAT on a digital voltmeter and reading off the value of the peak and of the points for the period 100 msec prior to stimulus onset. The mean value of the waveform voltage for this period was then subtracted from that of maximal peak amplitude to give values for the amplitude of component responses.

Computer averaging allowed the rapid and easy calculation of peak amplitude and latency values according to the rationale described above. The latency amd amplitude values of any peak in the waveform could then be measured. A variety of programmes were written which allowed the subtraction of separate waveforms obtained under differing conditions. A programmable Hewlett-Packard 7200A plotter was used to give analogue representations of the digital waveforms, and to plot graphs of VEP scalp distribution. All other relevant technical details will be given in the experimental chapters.

2.4:- Data representation

VEPs can be quantified in terms of peak-to-peak amplitude or peak latency, indeed this method will be employed in this study. However in many cases it will be necessary to show the VEP waveforms themselves, particularly where the time course of activity or the temporal relationship between VEP components of the same or differing cortical origin are of interest.

Chapter 3: Temporal integration of contrast stimuli

Introduction

The relationship between the duration and mean luminance of light flashes that can just be detected has been the subject of many psychphysical studies. Bloch (1885) had shown that the threshold for such stimuli remains constant if presentation times are less than some critical duration (r). The law which takes his name states that-:

$$It=K \text{ ,for } t < 'r'$$

(where I=intensity ,t=stimulus duration K=constant and 'r' is some critical duration). It has been shown to hold under a variety of conditions (see for example Graham & Kemp,1938; Barlow,1958; Kahneman,1964; Regan & Tyler,1971).

That this law should hold at all implies that there is a critical period for which intensity responses can be integrated before reaching threshold. The length of this critical period has been shown to vary as a function of a number of stimulus parameters including adaptation level (Graham & Kemp,1938; Barlow,1958; Roufs,1974) and stimulus chromaticity (Sperling & Jollife 1965; Regan & Tyler,1971). However for unpatterned achromatic stimuli an integration time constant of approximately 100 msec has been reported (Henrick,1956; Barlow,1958; Blackwell,1963). There appears to be no lower limit to the law as Baumgardt & Segal (1946) report that it holds for stimulus durations as low as $4x10^{-7}$ seconds.

Bloch's law has also been shown to hold in the contrast domain where Kulikowski (1977b) reports an integration time of 50 msec for sine wave gratings from 5-15 cpd. A significantly longer value has been reported by Kahneman (1964) for tasks involving high visual acuity, whilst Breitmeyer (1977) and Legge (1978) have reported that integration time increases with higher spatial frequencies, (see chapter 7). The dependence of the critical period upon stimulus conditions implies that the integrative processes lie at some post receptor site; the psychophysical functions reflecting therefore some form of neural summation (Boynton,1973). Neurophysiological data does indeed support this assumption, as Levick & Zacks (1970) report an integration time constant for Cat retinal ganglion cells of a approximately 64 msec. The higher values reported psychophysically for

contrast stimuli may therefore reflect integration at more central levels. The experiments reported in this chapter were conducted in an attempt to answer this question.

Previous studies of the temporal integration in the contrast domain have reported Bloch's law to hold for the amplitude of VEPs elicited by pattern-onset with an integration time constant of approximately 50 msec (Spekreijse et al,1973; Kulikowski,1977a).

In Spekreijse et al's study the major negative potential of the lower field pattern onset VEP (assumed to be CII) was examined. However in both studies the applicability of Bloch's law was assessed only in relation to VEP amplitude. A gap exist therefore in our understanding of the transmission of contrast signals through the primary visual pathways.

Preliminary experiments had suggested that the peak latency of the CI component was little affected by a reduction in the duration of a briefly presented stimulus, even for values close to duration threshold, thus implying a departure from the relationship predicted by Bloch's law. This finding appeared to be consistent with the data of Galletti et al (1979) who found that the response latency of cortical cells of simple and complex type, in the cat, remained constant with decreasing stimulus duration but increased with decreasing stimulus contrast. One might predict therefore that whilst contrast/duration reciprocity should hold for component amplitude this would not be the case for component peak latency. A clear dissociation between the parameters that determine the behaviour of these two basic properties of the VEP may provide some clues as to the nature and locus of the mechanisms underlying the psychophysical functions.

3.1:- Experiment 3.1a:- Bloch's law and CI

Methods

The stimulus for these experiments was a checkerboard with vertical and horizontal checks; check width was 10.5' arc. The contrast values were 0.3,0.15 and 0.075 and stimulus duration was varied from 150 msec to threshold duration. The method of contrast manipulation was described in chapter 2. The data are for four subjects.

Results

In figures 3.1a&b. are plotted for each subject CI amplitude as a function of the log of the (contrast x duration) product for the three levels of stimulus contrast used. It is clear from these graphs that stimuli with constant (contrast x duration) products, evoke equivalent amplitude responses and this is the case for a range of such products. Moreover the slope of the amplitude function when extrapolated to the baseline predicts very closely the psychophysically determined duration threshold. The value of 'r' implied by this data is 50 msec, beyond this limit stimulus contrast and duration cannot be reciprocally interchanged; the open symbols not fitted to the curve are for stimulus durations longer than 50 msec. The contrast equivalent of Bloch's law clearly holds for the amplitude of the component.

Typical examples of the VEP waveforms recorded under these conditions have been presented in figure 3.2, for the case where stimulus contrast was held constant and duration varied. In figure 3.3 are presented for two subjects the waveforms elicited by a constant duration stimulus varied in contrast over varied over a 1.4 (HD) or 1.75 (MJM) log unit range. In figure 3.4 are shown typical VEPs elicited by stimuli having approximately constant (contrast x duration) products.

A comparison of the waveforms presented in these figures clearly indicates that a reduction in the duration of a constant contrast stimulus produces a simple decrease in the amplitude of the resultant potential but its peak latency remains constant even at stimulus durations close to threshold. It appears that when stimulus duration is held constant, VEP peak latency is determined by physical contrast only; Bloch's law is therefore not applicable as is shown in figure 3.5 where peak latency has been plotted as a function of stimulus duration at each contrast level. In figure 3.6 are plotted peak latency values for each subject as a function of the Log of stimulus contrast for a 100 msec duration stimulus. For all subjects, latency increases by approximately 30-35 msec over a 1.4 log unit range with subject MJM showing a 40-45 msec latency increase over a 1.75 log unit range.

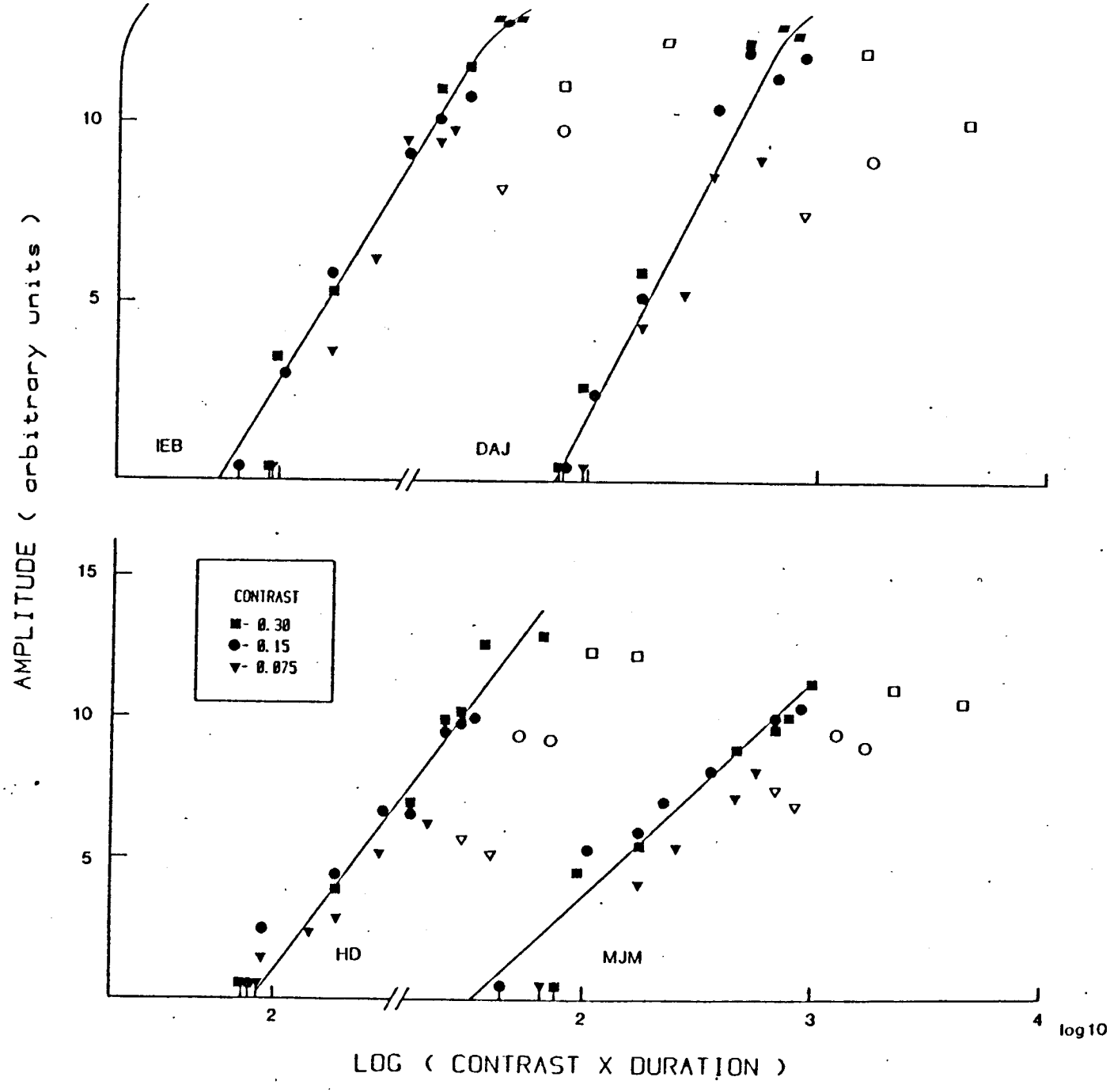
3.2:- Consistency of the VEP

A common criticism of VEP studies is the lack of repeatability of the recorded potentials and the difficulty in the reliable identification of stimulus related activity. Such a criticism would

Figure 3.1a

Plots of amplitude of CI as a function of the log (contrast x duration) product for contrast values of 0.3 (■), 0.15 (●) and 0.075 (▼). Durations up to and including 50 msec are represented by solid symbols and those for 70 msec and above by open symbols.

Also shown in this figure (upper) are data for CII. See section 3.4.


AMPLITUDE (arbitrary units)
10
5
IEB
DAJ
15
10
5
CONTRAST
■- 0.30
●- 0.15
▼- 0.075
HD
MJM
2
2
3
4
log10
LOG (CONTRAST X DURATION)

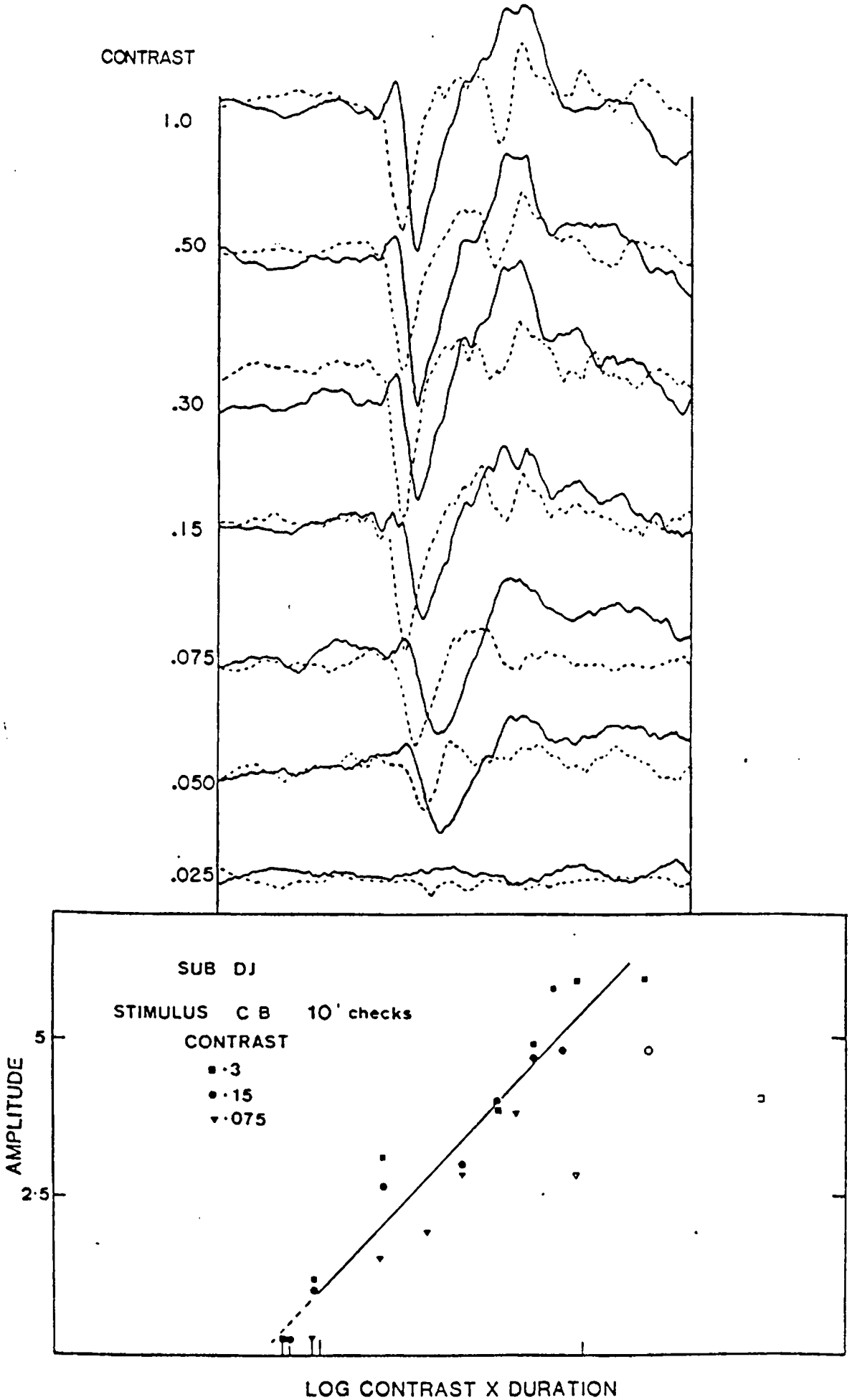
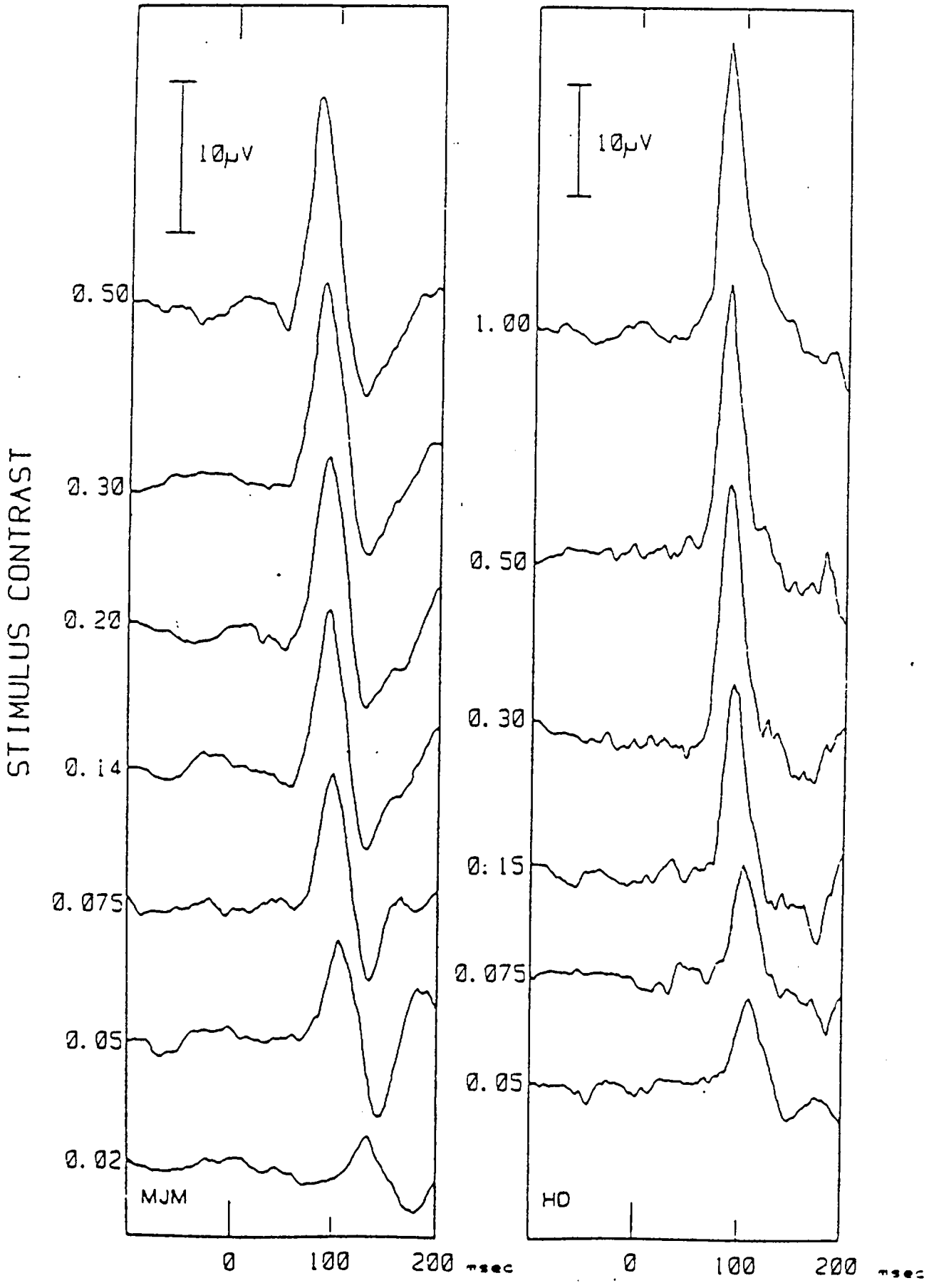


Figure 3.1b

Plots of amplitude of CI for subject D.A.J. as a function of log (contrast x duration). Also shown are VEPs elicited by a constant duration stimulus of variable contrast. In this figure CI has been reversed in polarity to indicate the temporal overlap of this component with CII.

Figure 3.3

VEPs recorded in two subjects to the left half-field presentation of a checkerboard of constant duration (150 msec) but variable contrast.



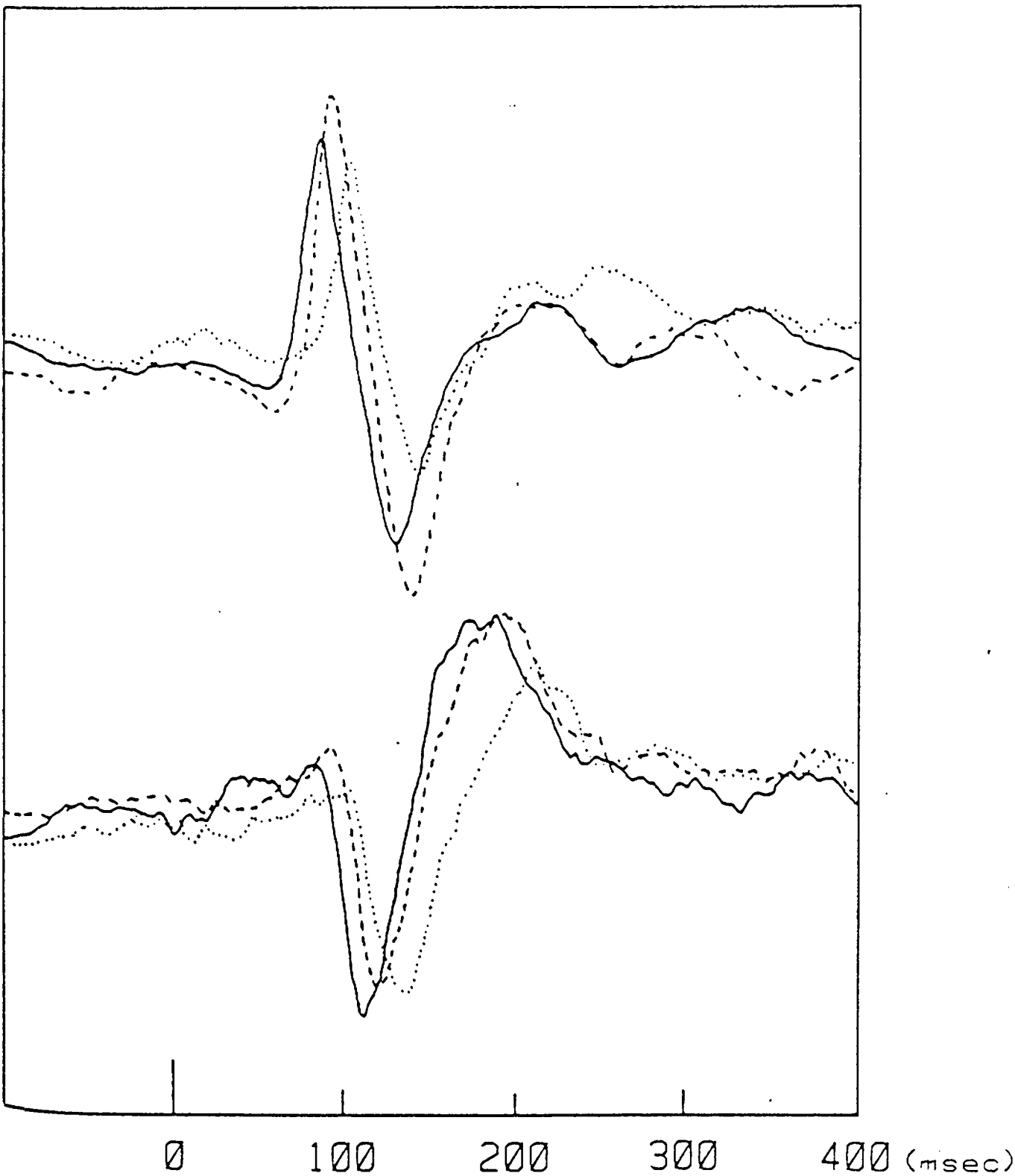


Figure 3.4

VEPs elicited by stimuli having approximately constant (contrast x duration) products.

'A' is for CI, 'B' for CII.

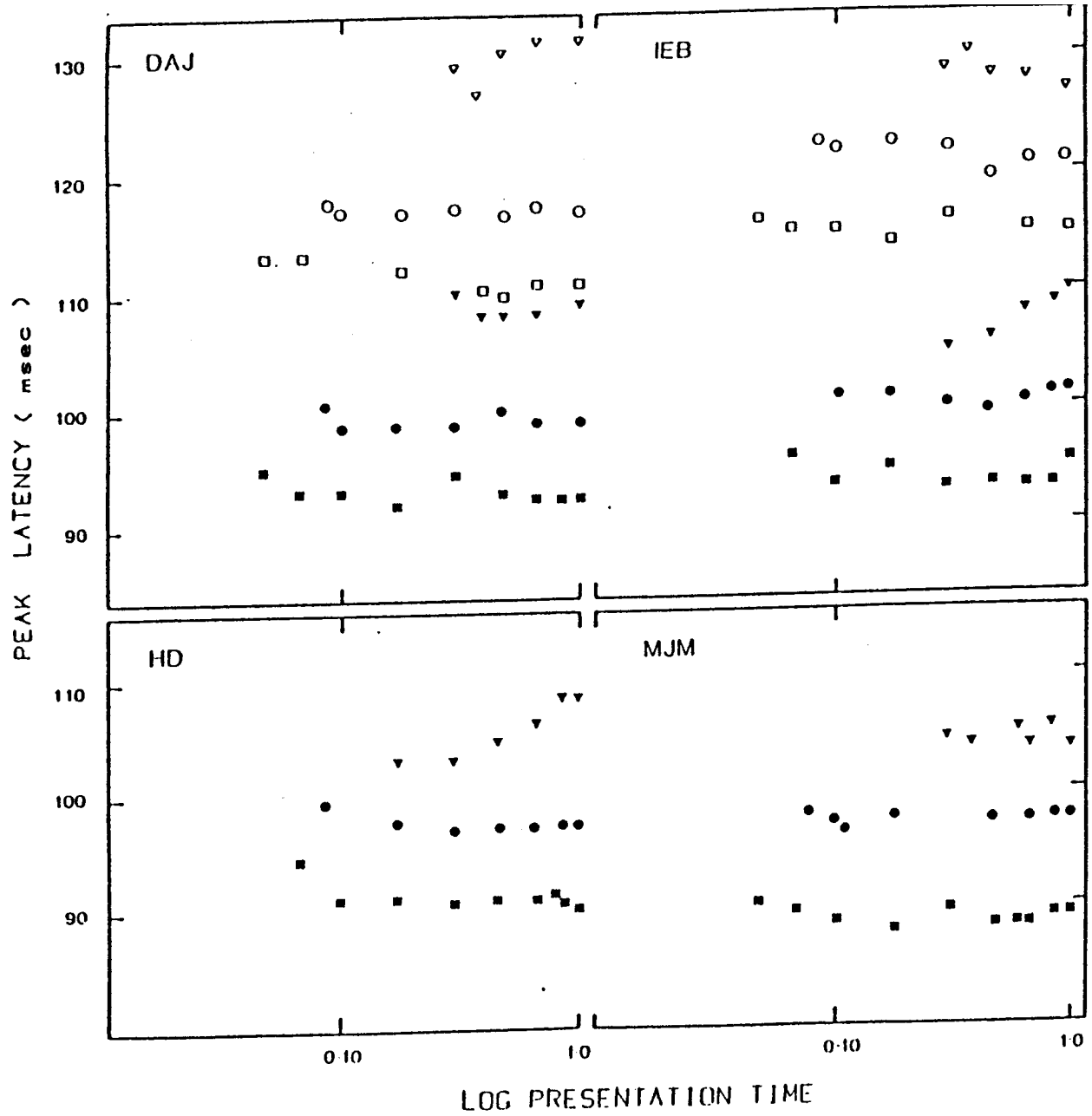
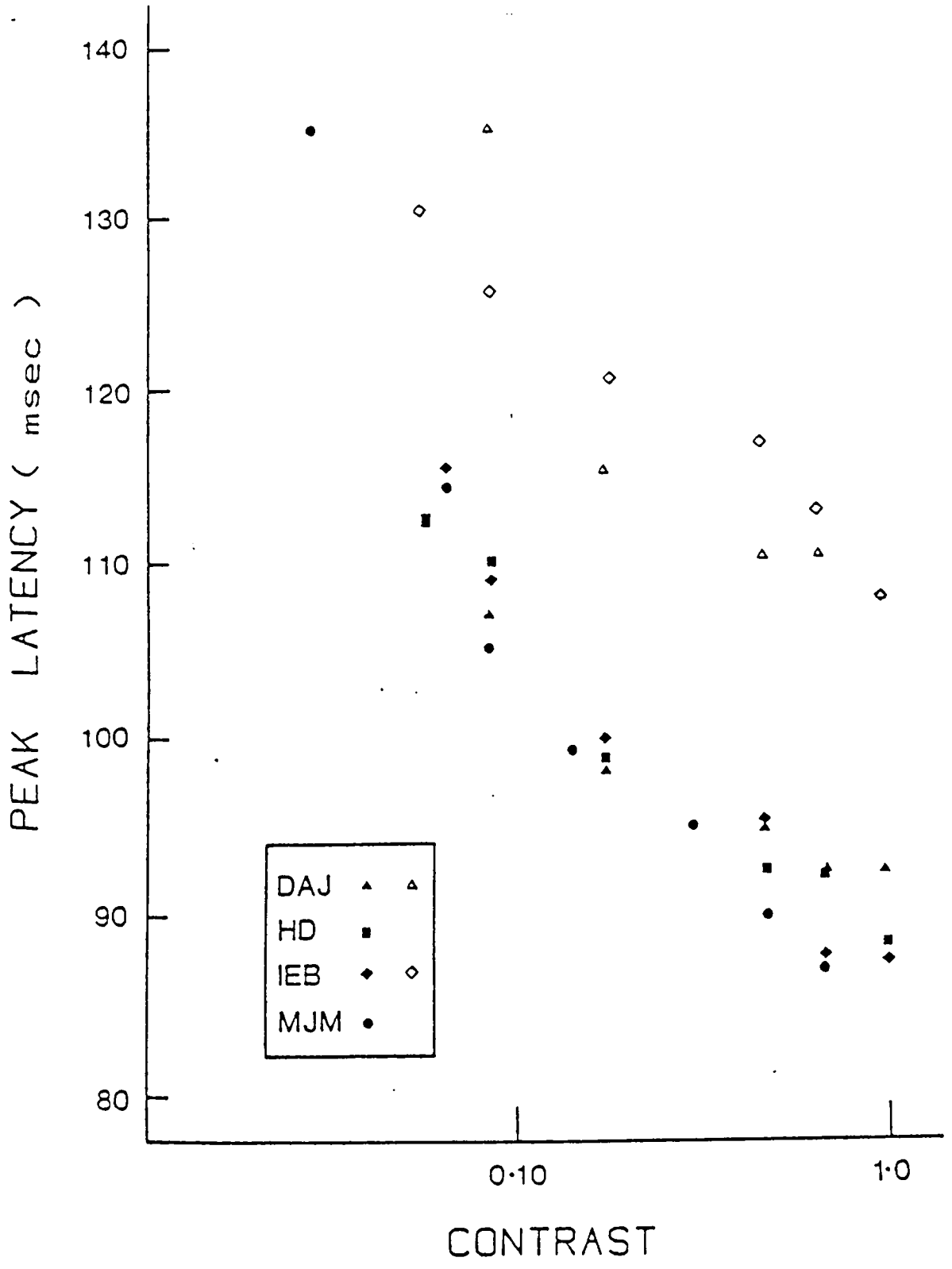


Figure 3.5

Plots of the peak latency of CI (closed symbols) and CII (open symbols, see section 3.4), as a function of stimulus duration for contrast values of 0.3 (■), 0.15 (●) and 0.075 (▼) for four subjects.

Figure 3.6

Plots of peak latency for CI (full symbols) as a function of stimulus contrast for a constant duration stimulus (150 msec). The open symbols are for CII (see section 3.4).



appear less applicable to the method of component analysis undertaken here. However it would be appropriate to give some indication of response variation which occurs from run to run since, as we are studying a physiological system, some degree of variability must indeed be expected. In psychophysical studies for example, it is well known that contrast thresholds show significant variation over time (DeValois,1978). In the present case the problem of response variation is a purely physiological one, in that we need to show that the effects described above are statistically reliable. To this end the following experiment was undertaken .

Experiment 3.1b

The stimulus and experimental conditions were similar to that reported in experiment 1a, except that in the present case the contrast of the checkerboard was set at 0.20 and only one subject participated in the study. Four runs of 30 sweeps were undertaken, each run being separately stored on disc. Stimulus duration was randomised from between 150 msec and threshold duration. However for durations at threshold, and below, 8 runs of 25 averages were undertaken.

Results and Discussion

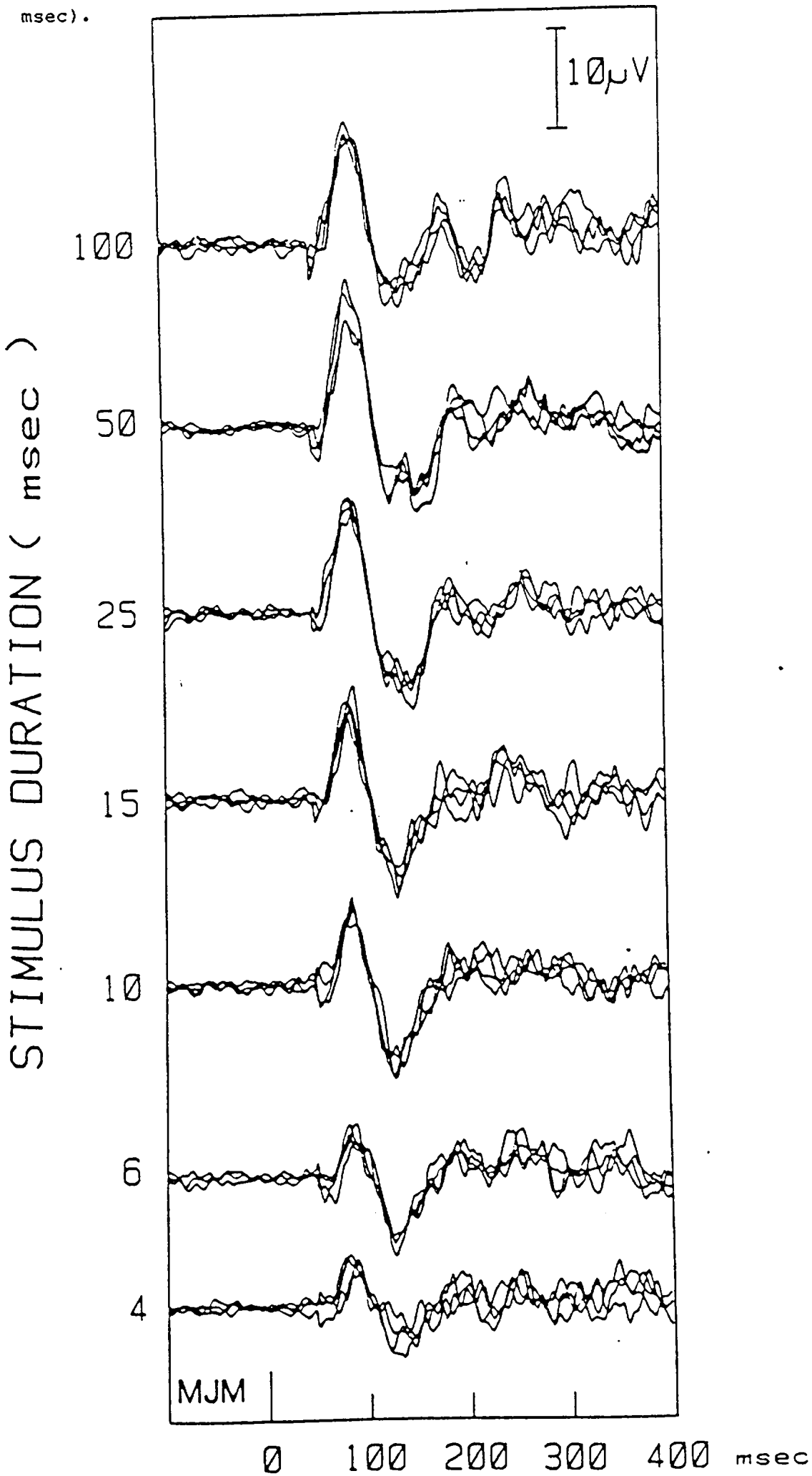
In figure 3.7 are shown the superimposed waveforms of the four individual runs undertaken at each stimulus duration. Also shown in this figure are the summed VEPs obtained by adding the four individual runs together. It is clear from these VEP waveforms that there is a very high degree of response repeatability, even for those VEPS obtained close to threshold. This point is made clearer by figure 3.8 where the mean amplitude and latency values of the component have been plotted as a function of the log of the (contrast x duration) product of the log of the stimulus duration, respectively. The vertical bars in each case indidicate +,- 1 SEM, the values being obtained by computer programme. The repeatability of this pattern onset component thus justifies the use of the method of 'run' summation used in experiment 1, and in subsequent experiments reported in this thesis .

3.3:- Experiment 3.2:- Bloch's law and CII

In this experiment the applicability of Bloch's law to the properties of the CII component will be studied. All stimulus values

Figure 3.7

Superimposed left half-field VEPs recorded to four separate batches of 25 presentations of the stimulus pattern of constant contrast (0.2) and variable duration. (Threshold duration is 2.5 msec).



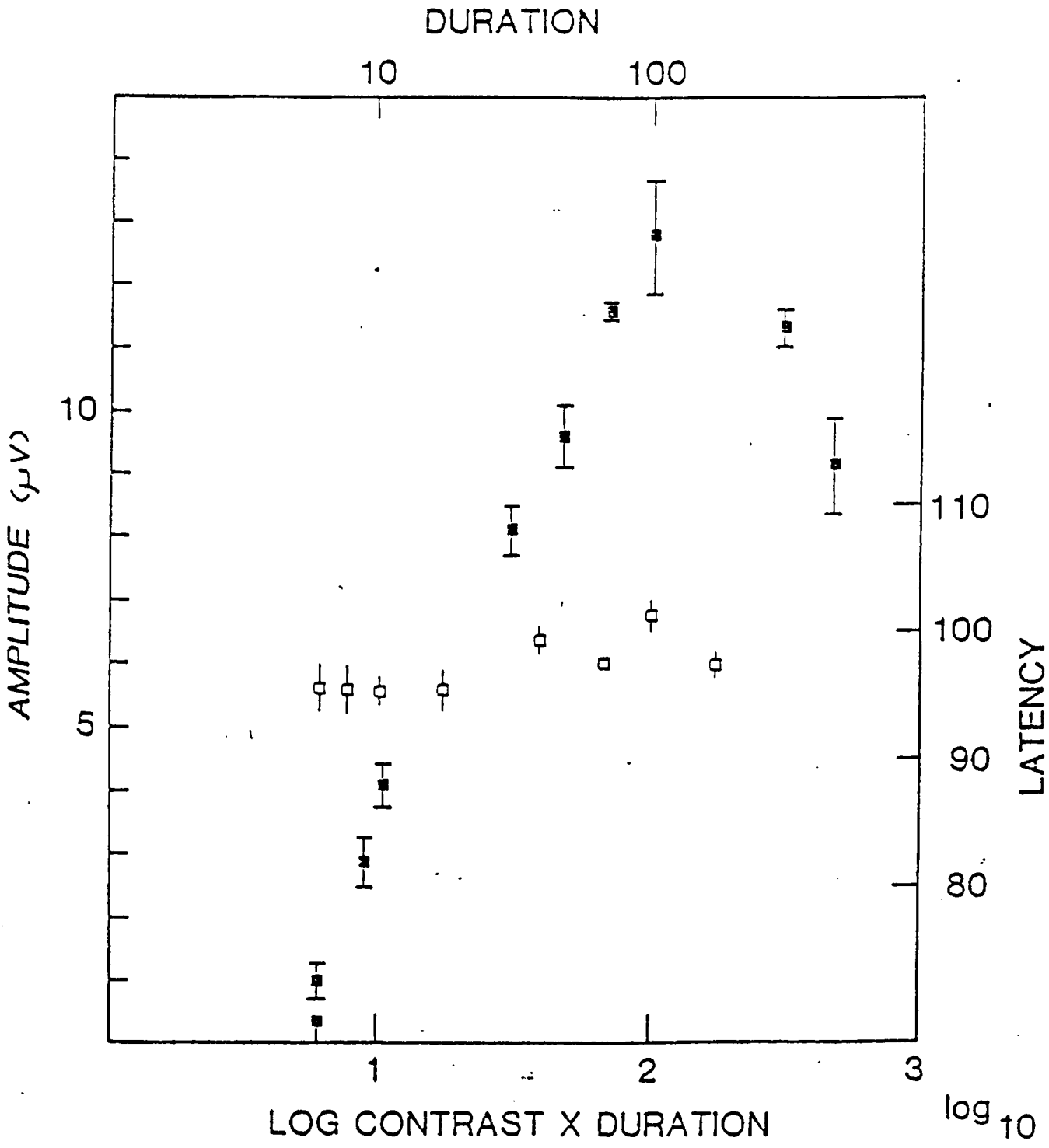


Figure 3.8a

VEP amplitude plotted as a function of log (contrast x duration) product for the 0.2 contrast checkerboard. Again the extrapolated slope closely predicts the psychophysical threshold (see text for discussion). Bars show +-1 SEM. For the most variable run, that at 50 msec duration, the mean amplitude is 12.78uv, with an SEM of 0.95uv. Plots of peak latency as a function of stimulus duration at a constant contrast (0.20). For the most variable case, that at 4 msec, peak latency is 92 msec with a +-1 SEM of 2.5 msec.

were as experiment 1a, although the pattern was now confined the lower half field and the VEPs recorded between a midline electrode 4 cm above the inion with reference to the right ear. Data are for two subjects only.

Results & Discussion

In figure 3.2b are presented typical waveforms elicited by a lower half-field stimulus of constant contrast and variable duration to illustrate the form of the response. Whilst in figure 3.4B are illustrated typical VEPs elicited by a range of stimuli with approximately constant (contrast x duration) products. These VEPs illustrate the form of the response.

As shown in figure 3.1 the amplitude of the CII component is logarithmically related to the (contrast x duration) product, the slope of the function predicting the psychophysically determined threshold, as was shown for CI in the same figure. The value of 'r' suggested by these results is again 50 msec, beyond this value the amplitude of the response levels off and reciprocity no longer holds. In figure 3.6 the latency of the CII component has been plotted as a function of stimulus contrast for a constant duration stimulus. It is clear that latency increases by approximately 30-40 msec over the 1.4 log unit range. Also plotted in this figure are the latency values for the same subjects of the CI component obtained in experiment 1(a). The curves run parallel to each other with a latency difference of between 15-20 msec, this value approximates the latency differences reported by Mitzdorf & Singer (1979) in a study which compared the difference in response time of excitatory synaptic potentials recorded in cortical laminae of area 17 and 18 of the macque monkey. The present component peak latency values are slightly on the high side, by about 5-10 msec; however two factors may explain this. The first is that Mitzdorf & Singer used an electrical stimulus applied to the primary afferent fibers at the optic chiasm and optic radiation as the evoking stimulus, the system's response to visual stimuli may therefore results in a slightly different temporal distribution of excitatory synaptic activity. Secondly there may be species difference in the latency of cortical activity. It is well known that such latency differences exist between cat and monkey (Lennie,1981); therefore these small differences between man and lower primate may be accounted by this fact.

3.4. Experiment 3.3 :- The effect of adaptation level

Introduction

It has been reported in the literature that the critical duration ('r') increases as background luminance decreases (see for example, Graham & Kemp,1938). Much of the data on which the assertion is based, however, has been obtained with unpatterned stimuli and it is possible that the detection under these conditions may involve mechanisms different from those which play a role in the detection of patterned stimuli. To increase our understanding of the processes underlying the generation of these components it was decided to examine the effect of luminance level on the integration time constant of the cortical contrast detecting mechanisms.

In the only known single unit study which had addressed itself to this question Levick & Zacks (1970) reported that the integration time of cat retinal ganglion cells was independent of adaptation level over a 5 Log units within the scotopic range.

Methods

Only two subjects were used in these experiments since it was necessary to increase the number of averages undertaken at the lower adaptation level which in turn increased the duration of the experiment from 3.5 to 4 hours. The stimulus pattern was also changed from a regular to a radially expanding checkerboard because such a pattern has lower contrast and duration thresholds which remain essentially constant throughout the whole of the patterned field; presumably reflecting the increase in receptive field size with increasing eccentricity (Anstis,1974). Two levels of background luminance were used: 500 cdm^{-2} and 3 $cdms^{-2}$. At the highest adaptation level, contrast values of 0.3, 0.15 and 0.075 and were used for sub MJM and 0.3 and 0.075 for sub HD. At the lower adaptation level it was necessary to increase stimulus contrast in order to increase the range of stimulus durations over which it was possible to record VEPs above noise level. Therefore for subject MJM contrast levels of 0.5, 0.25 and 0.125 and were used whereas for sub HD values 0.50 and 0.20 were used.

Results

In figure 3.9 a-b the amplitude of CI has been plotted as a

Figure 3.9a

Plots of amplitude as a function of log contrast x duration product at two levels of background luminance. Slope A is for the high adaptation level, slope B for the low adaptation.

Contrast values are:-

(■) 0.30

(●) 0.15

(▼) 0.075, for the high adaptation level, and

(■) 0.50

(●) 0.25

(▲) 0.125, for the low adaptation level.

There is no apparent increase in the critical duration with decreasing luminance.

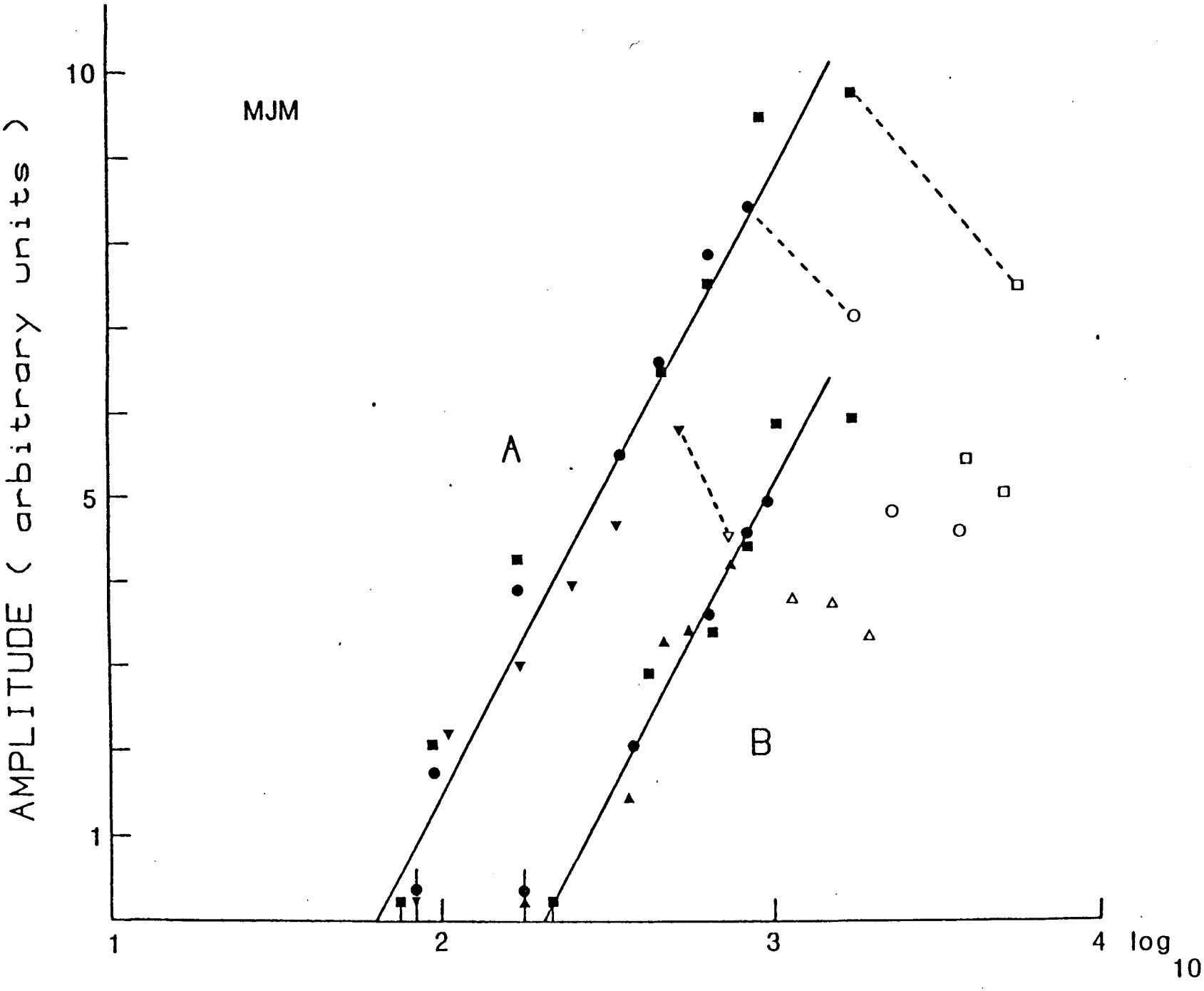

MJM
AMPLITUDE (arbitrary units)
10
5
1
A
B
1
2
3
4
log 10
LOG (CONTRAST X DURATION)

Figure 3.9b

As for figure 3.9a, but in this case for a second subject H.D.. In this case the contrast values are:-

(■) 0.30

(▼) 0.75, for the high adaptation level, and

(■) 0.50

(▲) 0.20, for the low adaptation level.

With this subject there is some suggestion that at the low adaptation level contrast/duration reciprocity holds for component amplitude for stimulus duration longer than 50 msec (see text for more detailed discussion).

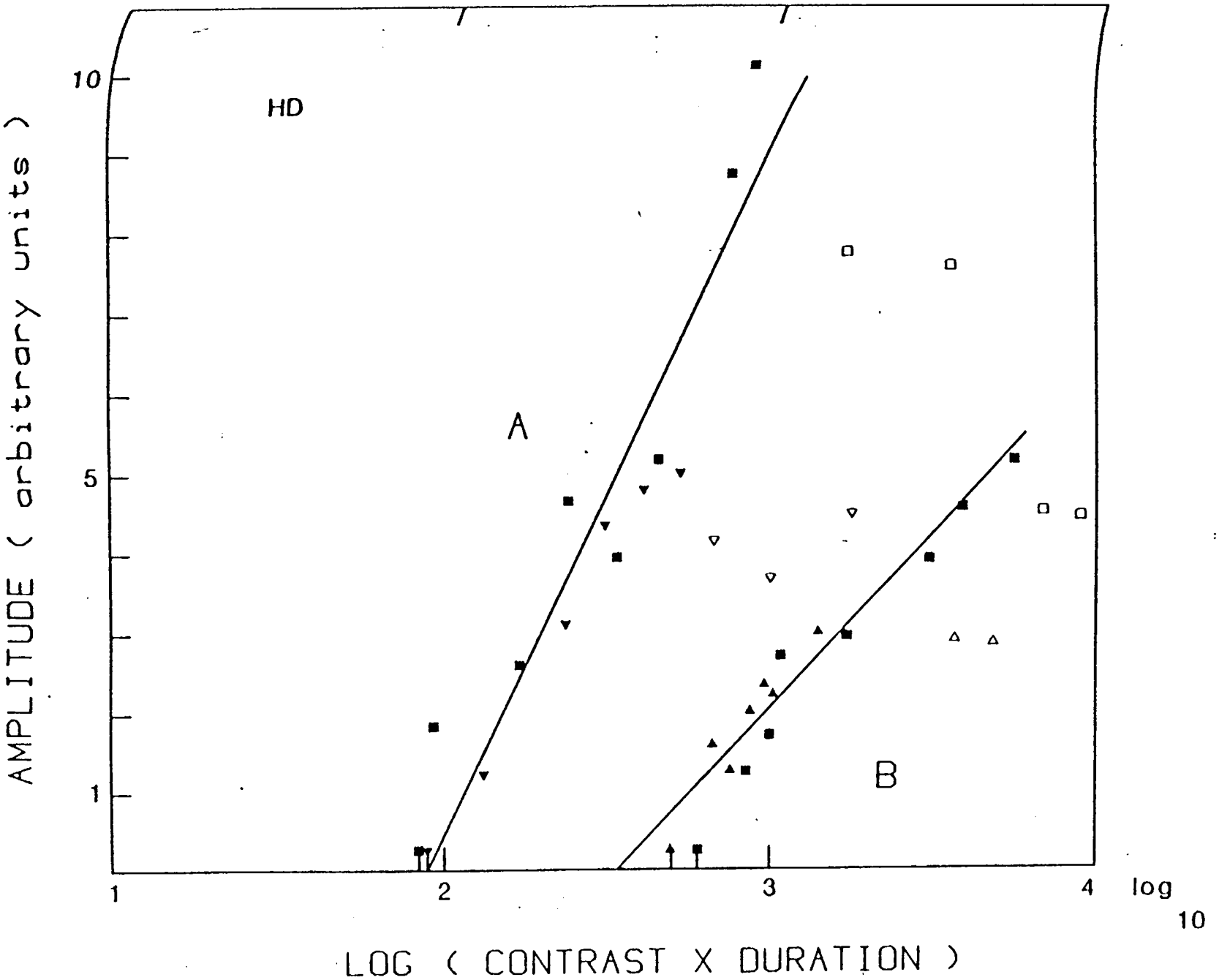

HD
A
B
10
5
1
AMPLITUDE (arbitrary units)
1
2
3
4
log
10
LOG (CONTRAST X DURATION)

Figure 3.10

VEPs recorded to left half-field stimulation by a radially expanding checkerboard at background levels of 500 cdm^{-2} (continuous trace) or 2 cdm^{-2} (dotted trace) at contrasts of 0.30 and 0.25 and the value of the calibration bars 10uv and approximately 5uv for high and low background levels respectively.

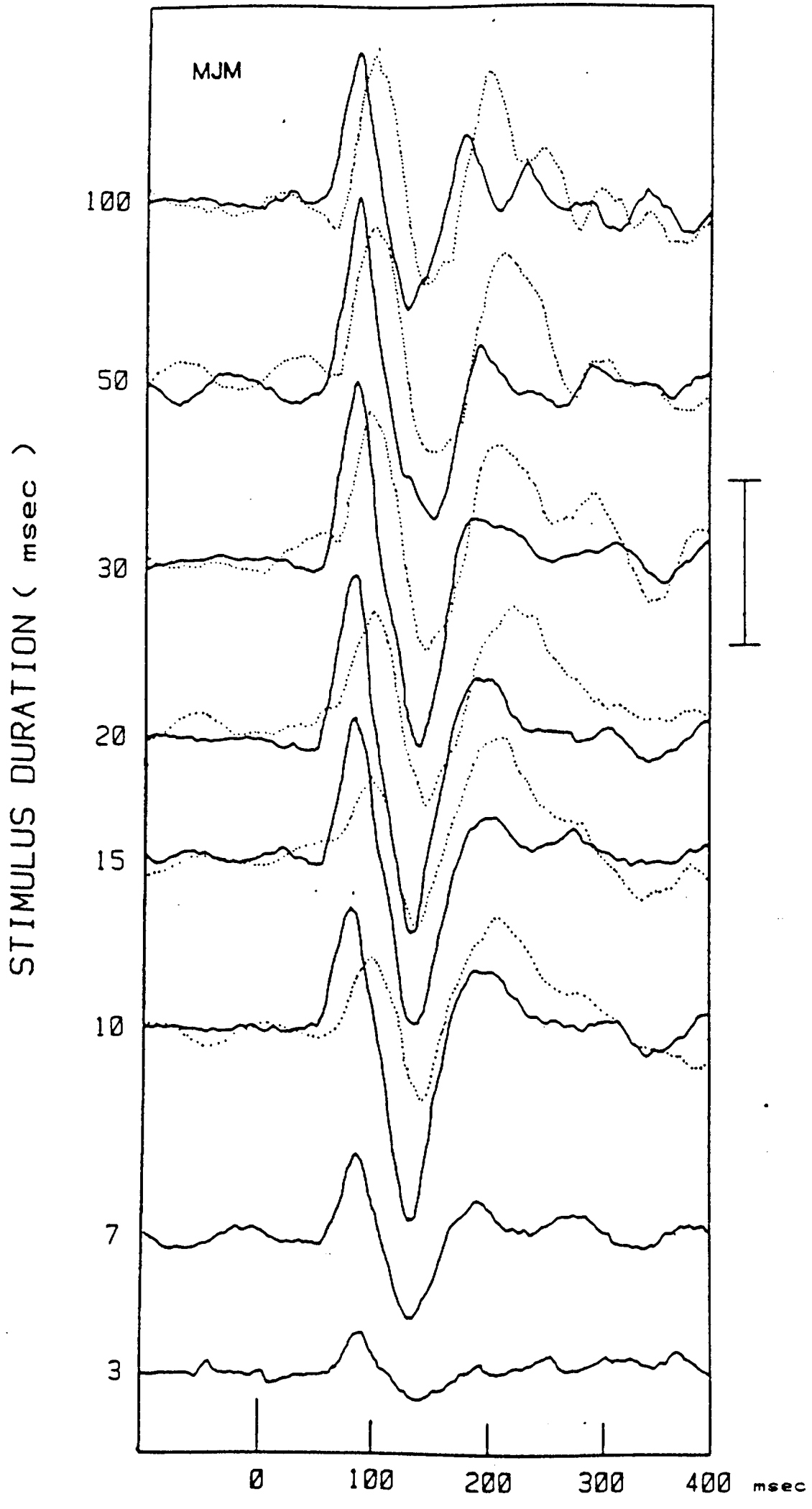

MJM
100
50
30
20
15
10
7
3
STIMULUS DURATION (msec)
0
100
200
300
400
msec

Figure 3.11
From Levick & Zacks (1970).

function of the Log of the contrast/duration product for the two adaptation levels for both subjects. Two major features are evident. The first is that a reduction in background luminance causes a decrease in the absolute amplitude of the evoked response (a fact that has been long known in VEP research) although, as has been pointed out by van der Tweel (1979), the actual decrease is relatively small.

The second and perhaps the most significant feature is that there appears to be no increase in the integration time constant despite the 2.5 Log unit decrease in adaptation level. For sub MJM this result is clear cut as the open symbols are for stimulus durations all in excess of 50 msec at both levels. However for subject HD at the lower adaptation level stimulus durations slightly in excess of 50 msec can be fitted to the curve, although this is only true for durations up to 70 msec and by 100 msec the amplitude has again levelled off. In figure 3.10 are shown typical waveforms recorded at high and low adaptation levels, these VEPs indicate that luminance level itself has the effect of adding a constant to the peak latency value. Therefore Bloch's law is again not applicable.

3.5:- General Discussion

The main finding of these experiments is the dissociation of the parameters that determine component amplitude and latency functions. It has been found that the contrast equivalent of Bloch's law holds for the amplitude of both the CI and CII components with an integration time constant (r) of approximately 50 msec. Such a value is consistent with the evoked potential data of both Kulikowski (1972) and Spekreijse (1973) and is equivalent to the psychophysically determined value of 'r' obtained by Kulikowski (1977) for sine wave gratings of 5-15 cpd. By contrast, the latency of these VEP components does not conform to Bloch's law being independent of stimulus duration, and determined by stimulus contrast alone, such that over a 1.4 log unit range it increases by approximately 30-35 msec. A comparable increase in peak latency discharge over an equivalent range of stimulus contrast been reported for units in both the LGN (Baker et al,1969) and area 17 and 18 of the cat visual cortex which supports the present data and in turn questions the interpretation which has been placed on the dramatic increases in both human (Breitmeyer,1977; Harworth & Levi (1977) and monkey Harworth et al (1979)) reaction times to briefly presented patterned stimuli as a function of decreasing stimulus contrast. This

finding would suggest that the results of such studies cannot be unequivacally interpreted as reflecting the conduction velocity of afferents below the primary visual cortex as Breitmeyer (1977) has proposed, (see chapter 7).

The absence of contrast/duration reciprocity for component peak latency is similar to a phenomenon that has been observed in the post-stimulus time histograms of cat retinal ganglion cells where a reduction in the duration of a constant intensity stimulus is found to produce a decrease in the magnitude of unit discharge, but leaves the latency of maximal discharge unaffected (see figure 3.11, Levick and Zacks,1970).

The phenomenon is also observed at the level of the LGN. Baker et al (1969) report that whereas (below a critical duration of 40 msec) stimuli having constant (contrast x duration) products evoke unit discharges of equal intensity, the latency of peak discharge was, in every case longer for lower contrast stimuli irrespective of the resulting contrast/duration product (see figure 3.12). Baker et al speculated that these consistent although small latency differences (some 15-20 msec between the highest and lowest of the contrast values used in that study) would be of little functional significance since further integration, at or prior to, the cortex itself would result in smearing which erodes them. The present data suggest that in man at least such is not the case. Whilst there may be no psychophysical correlate of this electrophysiological fact, which may indeed be of little functional significance, it nevertheless suggests that different mechanisms are determining the two functions.

To my knowledge, there is no available data on the applicability of Bloch's law to the impulse response of single units in the visual cortex of either Cat or Monkey. However Galletti et al (1979) have reported that single units in both area 17 and 18 of the Cat do not show an increase in the latency of maximal discharge as a function of decreasing stimulus duration. They do however show a latency increase of approximately 30-35 msec when stimulus duration is held constant and stimulus contrast is reduced over a 1.3 Log unit range (see figure 3.13). Galletti et al's failure to find a decrease in the amplitude of peak discharge with the shortest stimulus duration used in that study was probably due to the fact that the physical contrast of the stimulus was well above the level at which the sampled cell population showed response saturation; an effect also observed for CI. For example in

Figure 13.12

From Baker et al (1969).

Response of single cells in the cat LGN to stimuli of constant contrast/dration products. Notice discharge latency is an approximately linear function of log contrast, with values quantitatively similar to that found for CI and CII.

Figure 13.13

From Galletti (1979). Response of cortical cells to stimuli of varing duration, and contrast. See text for further discussion.

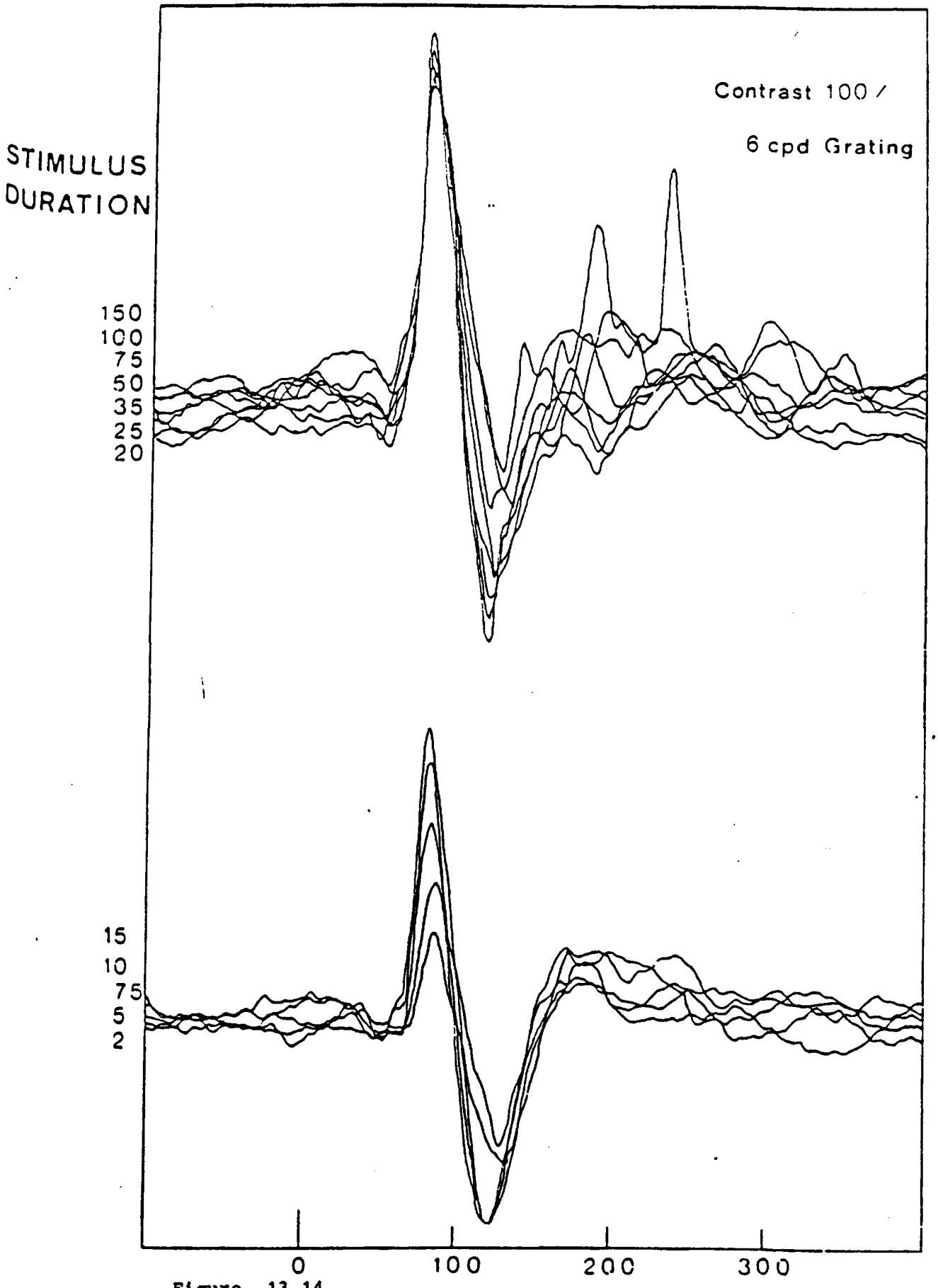


Figure · 13.14

VEPs elicited by the left half-field presentation of a 6 cpd square wave grating of 1.00 contrast.

At durations above 15 msec VEP amplitude remains effectively constant, the 'off' response can also be observed at these higher contrast level with longer stimulus duration.

For shorter durations peak amplitude progressively decreases

figure 3.14 are shown the waveforms elicited by a 6 cpd square wave grating of 1.00 contrast varied in presentation time 150 msec down to threshold duration, at presentation times greater than 20 msec the amplitude of each potential has a similar value. It is not until presentation time is less than 20 msec that VEP amplitude begins to decrease. In Galletti's study, stimulus duration was never less than 20 msec. Thus there is no disagreement between the VEP and single unit data.

The results of experiment 3 suggested that the critical duration over which response amplitude showed contrast/duration reciprocity is independent of background luminance at least over the 2.5 log unit range used here. The result was somewhat unexpected in the light of the psychophysical data. However the limited single unit data for the cat (Levick & Zacks,1970) are consistent with the present findings in showing that for retinal ganglion cells the critical duration over which discharge amplitude showed intensity/duration reciprocity (reported to be approximatly 60 msec) was independent of background luminance over a 5 log unit level in the cat scotopic range. As is evident from fig 3.10 reducing background luminance simply shifts the slope of the amplitude function bodily along the abscissa, as would be expected from the increase in both contrast and duration thresholds that occurs at lower adaptation levels. The increase in overall peak latency and the decrease in the absolute amplitude of the contrast VEP under similar conditions has been previously reported (Van der Tweel,1980; Halliday,1977) although it should be noted that the actual decrease in absolute amplitude over the 2.5 log unit range is suprisingly small.

Spekreijse et al (1973) have suggested that with decreasing luminance level and/or contrast the waveform becomes more "sluggish". There is little evidence for this in the present data which in turn supports the findings of Van der Tweel (1980) who reports that if at each adaptation level the physical contrast of the stimulus is a fixed multiple of threshold contrast, then the shape and amplitude of the waveform changes very little even over a 5 log unit adaptation range. The results of experiment 3 support Van der Tweel's conclusion that for response latency at least, the principal effect of a reduction of stimulus contrast and/or luminance level must be determined at levels distal to the site of the VEP generator. Indeed, it would appear that the bulk of the increase in visual latency must arise in the retina itself. Kuffler (1953) has shown that the latency for which retinal

ganglion cells discharge can be increased as a function of decreasing luminance is 15-93 msec. Whilst Levick & Zacks (1970) report a 9.5 msec increase in latency per log unit decrement in background luminance within the cat scotopic range . In comparison to these values are those reported by Bishop (1965) who found an increase of only 7-9 msec in response latency of Cat LGN units when varying strengths of electrical stimulation were applied to the Optic Tract. In conjunction, these results and those of Levick & Zacks (1970) and Baker et al (1969) suggest that much of the critical duration is determined by neuronal interactions shortly succeeding the receptors themselves and that there is little modification as the signal is transmitted through the visual system to the primary visual cortex.

In summary, these experiments have shown that there is a dissociation between the parameters that determine the intensity and the temporal distribution of neuronal activity within the human visual cortex. The implication of this finding is that for the visual system there exists only a partial equivalence, in terms of its electrophysiological response, between stimuli that can be shown psychophysically to produce comparable sensations.

This conclusion does not necessarily imply that there is no relationship between subjective experience and neuronal activity at this level, obviously there is, as one aspect of the present data clearly indicate, ie, as subjective contrast decreases with decreasing stimulus duration so does component peak amplitude, the function produced predicting very closely the psychophysical threshold.

Whilst it may be possible to construct a metric to measure subjective sensation (magnitude estimation tasks for example) which may correlate with the functions describing gross neuronal discharge (Stevens, 1976), it is more difficult to design a behavioural task which could adequately assess the correlation between the latency of peak discharge (assuming this feature of the response was of some prime significance with regard to stimulus processing) and the latency of visual sensation.

Simple reaction time is perhaps the most obvious candidate and indeed data reviewed by Mansfield (1973) does suggest that the latency of RT's is little changed with decreasing stimulus duration and thus reduced subjective intensity, at least for durations above approximately 10 msec. The studies reviewed however were undertaken

with unpatterned stimuli presented as luminance increments, they cannot therefore be compared directly with the results of these experiments. An increases in simple reaction time is however difficult to interpret as it is the latency of the whole system that is being measured as opposed to latency within or between specific stages of that system. Indeed it has been noted above that there is a lack of correlation between electrophysiological and psychophysical measurements of visual latency. Whilst there are difficulties in making comparisons across studies, at least with regard to absolute measurements, the present discrepancy, which amounts to several orders of magnitude, suggests that the interpretation placed on the psychophysical results is in fact wrong. That is, they do not primarily reflect latency of conduction velocity of afferents within the primary visual pathways as has been suggested by Breitmeyer (1977) and Harwerth et al (1977; 1978).

However, data does exist to suggest a reasonable agreement between simple reaction time and VEP component peak latency. Czigler (1976) has shown that for patterned stimuli of variable physical contrast, latency of reaction time shows a similar function to that obtained for the CI component (although the range of contrast values used extended over only 0.8 log units at the suprathreshold end of the scale) and further the component was not studied under conditions which totally isolate it from succeeding activity, with which it may have interacted (see Jeffreys,1980). Clearly more data is needed on this question, preferably combining simultaneous electrophysiological and psychophysical measurements of response latency on the same subject, particularly if as here, VEP components can be effectively isolated.

The available evidence does suggest however that there is a greater increase in response latency (both behavioural and electrophysiological), when physical as opposed to subjective contrast is reduced. It may be the case therefore that the lack of stimulus equivalence (in terms of response latency) for these VEP components and for single units in the cat may have a counterpart in visual latency measurements obtained psychophysically.

As the major response properties (ie intensity of firing, latency of discharge, onset latency and duration of response) of single units at the cortex and LGN of the cat show qualitatively similar properties to the components of the pattern onset VEP it would appear that the mechanisms that determine the dissociation between the latency and intensity of neural discharge must reside if not within, then shortly

succeeding, the photoreceptors themselves. One must await the results of single unit studies in order to determine the exact relationship between the response of cortical units and the applicability of the contrast equivalent of Bloch's law. However, as the preliminary studies by Galletti et al (1979) have shown that the response latency of cells within the cat visual cortex is independent of stimulus duration but not of stimulus contrast, it would be logical to expect that when the appropriate studies have been undertaken the response of single units will be consistent with the VEP data.

Chapter 4:- Temporal resolution and summation of contrast patterns

Introduction

The experiments of the preceding chapter showed that the contrast equivalent of Bloch's law held for the amplitudes of both the CI and CII components of the pattern onset VEP, and that the integration time constant was approximately 50 msec was reported.

Temporal processing can also be studied by examining the response of the system to 'pairs' of briefly presented stimuli as the interval between their onset is progressively increased. This method, applied here in the time domain, is analogous to that used to specify the spatial resolving power of telescopes and other optical instruments and has been the subject of a number of pyschophysical studies. The majority of such studies have however used unpatterned stimuli, presented as luminance increments, and few have examined the limiting resolution for contrast stimuli (see Boynton,1973).

In this chapter the temporal properties of CI will be examined with brief discrete pairs of patterned stimuli of the same contrast polarity. Specifically, the limit of temporal resolution and the time course of temporal summation of this component will be studied. An attempt will also be made to determine whether the critical parameters which limit temporal resolution at the neural level are related either to the interval between the onset of brief pairs of patterned stimuli (SOA) or the interstimulus interval (ISI), (or a combination of the two). The study will be limited to the CI component, because it can be most effectively isolated from both preceding and succeeding stimulus-related activity.

4.1:- Temporal resolution

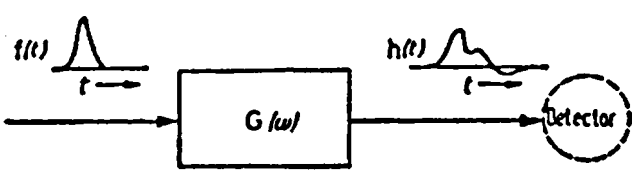
Many studies have examined what has been termed the "persistence of vision" (see for example Boynton,1973). These studies have primarily concerned with the properties of the system as revealed by its response to flickering stimuli with either a sine or square wave temporal luminance profile. A similar type of study has been conducted in the contrast domain with grating or checkerboard stimuli modulated in

counterphase about some mean contrast level (see for example Kelly,1973).

The results of such experiments are described in terms of the critical flicker frequency (CFF) which is the absolute value in Hz of the maximum frequency at which oscillation of the stimuli can be detected. For luminance stimuli, CFF has been shown to vary as a function of background luminance, stimulus size, retinal location, chromaticity as well as modulation amplitude, (Kelly,1972).

For contrast stimuli, in addition to the above mentioned variables, the spatial frequency of the contrast profile has also been shown to affect the CFF (see Kelly,1975). Specifically, stimuli with high spatial frequencies have lower CCFs than those in the medium range around 5-6 cpd. This effect is in contradistinction to that observed with low spatial frequency stimuli, where contrast threshold are lower when the stimulus is temporally modulated.

A number of models have been proposed to account for the data relating to the temporal transfer function of the visual system. The simplest model is similar to that illustrated in figure 4.1. Although no real system, particularly a physiological one, obeys the linear superimposition principle, the visual system appears to do so to a first approximation, particularly near threshold. The difficulties faced by such modelers are in specifying the transfer function on the basis of experimental data and, having specified it, attempting to relate it to known or postulated physiological mechanisms (see Kelly 1973 for review of the relevant problems and models).



Schematic representation of the linear model of flicker sensitivity, governed by the transfer function, $G(\omega)$

If a linear model is assumed however, then the transfer function, G(w), based on experimental data obtained under steady state conditions

should in principle be sufficient to predict the output for any periodic or transient input. Thus, for structureless stimuli, Roufs (1966) and Roufs and Melenbugge (1967) report that the threshold for rectangular pulses of variable duration, presented at a range of adaptation levels can be predicted from the relevant CFFs determined for each subject with flickering stimuli. However other data suggest a more complicated relationsip between CFF and double pulse threshold. Pieron (1961), for example, has argued that for pairs of pulses the limit of resolution is approximately twice that for a continuous series or flickering train; he further suggests three reasons as to why this may be the case.

> "The first is "... the facilitory influence of the increased duration of observation on the process of perceptual discrimination ..." The second ".... is the progressive sinusoidal regularity of the wave of excitation potential whose own evolution becomes independent despite all disymmetries of stimulation ..." [and the] third ...." is the progressive synchronisation of the periodic activities of the cellular ensemble".

The first factor is purely statistical, a manifestation of the higher probability of detection that results from an increase in the number of pulses presented.

The second factor draws attention to the fact that in the double pulse paradigm the initial pulse is likely to produce some unique response which, perhaps because to the longer duration of its associated neural activity, may interfere, with the response evoked by the second stimulus. This situation would not occur with a flicker train where the subject is adjusted to steady state conditions before making a judgement. The initial pulse of the train will not therefore adversely affect the determination of threshold.

Pieron's third factor is a little more nebulous, although the principle may underlie the results of some experiments which have shown a curious dissociation between psychophysical and electrophysiological (VEP) measures of CFF. For example, Van der Tweel & Lunel (1965) reported that for sinusoidally flickering stimuli, VEPs could be evoked by stimulus frequencies greater than the psychophysical determined CFF. They found that whereas the 'subjective' CFF was 40 Hz, VEPs could be

elicited by frequencies up to 70 Hz. These findings are supported by the studies of Spekreijse (1966) and Regan (1968) under different conditions.

It is possible that at these higher rates of oscillation, some populations of the neuronal ensemble become entrained to the frequency of visual stimulation. The resultant dissociation between electrophysiological and psychophysical measurements indicate that on some dimensions neural and subjective functions are not isomorphic. The gating of input from lower to higher levels is not uncommon and indeed is perhaps to be expected. Alternatively it may be suggested that VEPs, which sum activity of many neural responses, do so at these high repetition rates by integrating over a larger cortical area then the specific brain mechanisms which give us our perception of flicker (Regan, 1981).

The relevant data suggest therefore that the CFF for both luminance and contrast stimuli obtained under steady state conditions cannot be used to predict the limit of discrete double flash resolution. Few attempts have been made to study the properties of the pattern onset VEP under a double pulse paradigm and there is to my knowledge no published data on the relationship between the psychophysically determined limit of resolution and that of pattern onset VEPs despite the fact that such studies would be complementary to those which that have attempted to provide electrophysiological data on the process of temporal intergration within the visual cortex.

4.2:- Temporal summation

Psychophysical studies have shown that the visual system has the properties of a leaky integrator since the interval over which brief threshold stimuli show complete temporal threshold summation is significantly shorter than the interval over which single stimuli show complete temporal integration (see Roufs (1974) for detailed discussion)

If the components of the pattern onset VEP reflect the electrophysiological response of those neural mechanisms in striate and extrastriate cortex underlying the perception of contrast stimuli then their properties should resemble those functions obtained at both the physiological and psychophysical level.

4.3:- Methods and procedure

The stimuli used in these experiments were regular dot patterns of 16°arc diameter presented in the appropriate half field. Stimulus duration was either 10 or 2.5 msec and background luminance was either 500 or 2 $cdms^{-2}$. Both negative and positive contrast pattern pairs were used to provide a more comprehensive characterisation of component properties. The contrast of the negative pattern was 1.0. and in order that the positive pattern should have the same suprathreshold value at the durations used, the subject was instructed to adjust the luminance of the positive pattern elements until they had the same duration threshold which was approximately 1-1.5 msec.

4.4:- Psychophysical measurement of temporal resolution

Most studies of double pulse resolution have used brief unpatterned stimuli and the factors that limit their resolution may differ from those limiting the resolution of contrast patterns. Contrast patterns have after all an added dimension, the spatial period of the contrast profile, and it is likely that this could differentially affect the psychophysically determined limit of temporal resolution for brief discrete pairs as it does the CFF (Kelly,1973; see also chapter 7). In order therefore to make some more meaningful comparisons between the temporal properties of CI and the limit of subjective temporal resolution, I conducted a short psychophysical study of resolution under the same conditions as used in the VEP experiment.

4.5:- Psychophysical methods

Temporal resolution was measured by the method of ascending and descending limits (Kling & Riggs,1972), subjects were instructed to report either a single or double presentation. Starting with widely seperate pulses (i.e. 150 msec) confidently reported as a double stimulus, the SOA was then progressively reduced, in 5 msec steps, until the subject reported seeing only a single pattern. Threshold was then defined as midway between the last SOA and the immediately preceding one. The next series was then started well below this level (ie SOA 10 msec) and the onset interval increased until the subject reported seeing a double presentation. Two ascending and descending trials were undertaken for each of the six subjects and the mean value of all four trials taken as the limit of temporal resolution. This

limiting value was measured for stimuli of both 10 and 2.5 msec duration; the threshold duration for single pattern detection being 1 msec. Only the positive contrast pattern was used.

4.6:- VEP Results

In figure 4.2 typical waveforms have been presented for two of the three subjects for the range of SOA values at the high adaptation level for both negative and positive contrast pairs. In both cases for SOAs up to approximately 40 msec, the waveforms show a single clear peak, whose latency increases slightly, by (3-7 msec) for SOAs between 10-30 msec. For SOA's of 50 msec the VEP has two distinct peaks, and the latency values of each of these peaks corresponds to that predicted if in each case only one of the stimuli had been presented at the appropriate interval. In figure 4.3 are shown the waveforms recorded in two subjects for either negative (MJM) or positive (HD) contrast pairs presented at the lower adaptation level. Whilst in figure 4.4 are superimposed for SOAs of 10, 50 and 70 msec the waveforms obtained at both high and low adaptation levels for the 10 msec duration stimuli. Two features are evident. Firstly, as background luminance is decreased, there is an overall increase in peak latency of approximately 20 msec (see figure 4.4).

Concomitant with this increased latency of the response there is a decrease in the absolute amplitude of the VEP as is indicated by the respective calibration bars shown in figures 4.2 and 4.4. The effect of adaptation level on the major dependent variable, the limit of resolution, appears minimal. Indeed, a comparison of the waveforms for the high and low levels reveals no difference in the limit of component resolution since in each case the potential to the second of the pair is evident at 50 msec SOA. The limit of temporal resolution appears therefore to be independent of adaptation level at least from high photopic to mid-mesopic levels. The independence of response peaks at this onset interval suggest that the contrast detecting mechanisms of the striate cortex are treating the temporally independent stimuli as separate events.

4.7:- Psychophysical limit of resolution

In figure 4.5 are plotted as bar histograms the limit of subjective resolution obtained psychophysically. For each subject the mean limit of resolution for both the 10 and 2 msec stimuli have been shown. The limit for the 10 msec stimuli lies between 42.5 - 55 msec

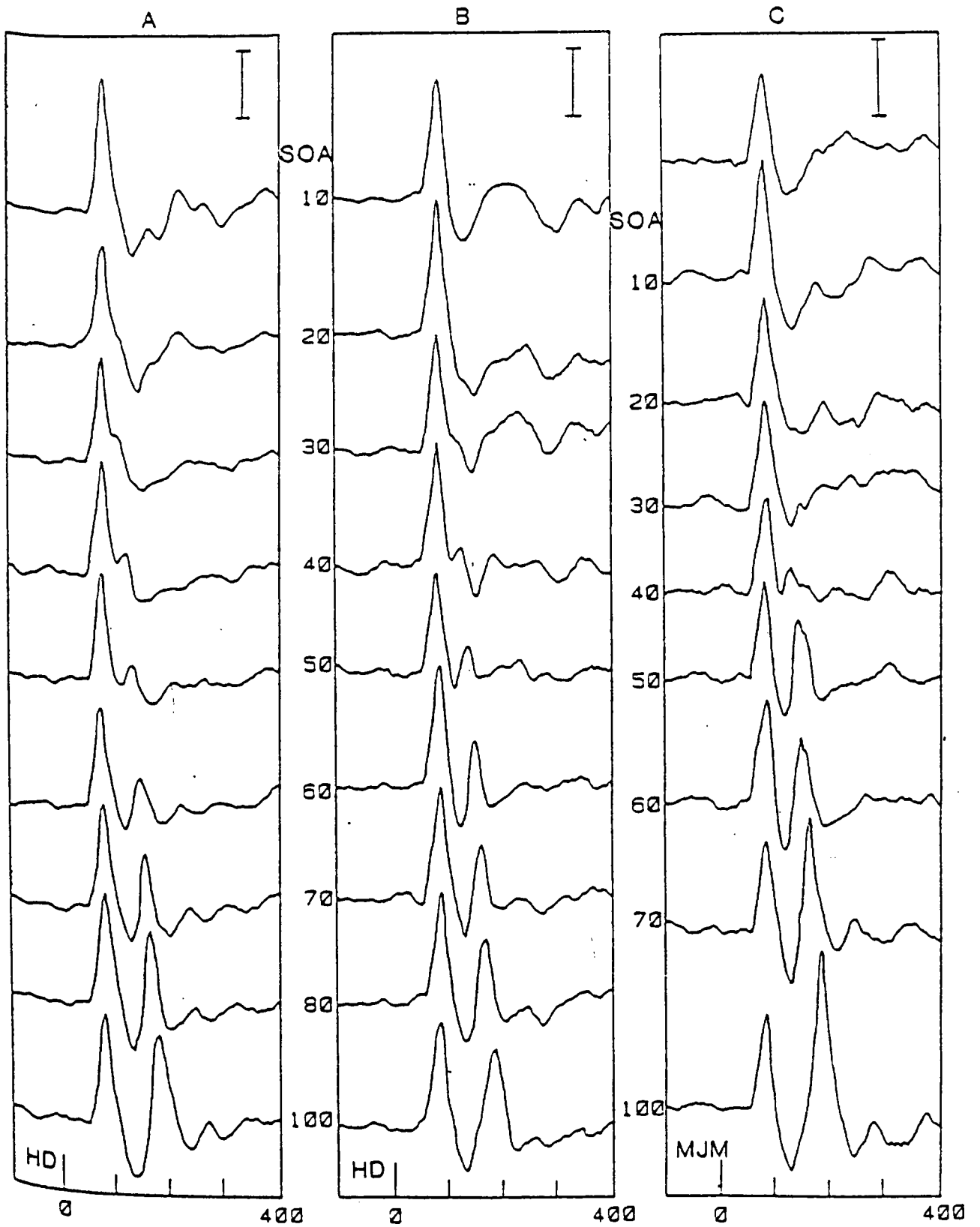


Figure 4.2

VEPs for two subjects under positive-positive (A) and negative-negative (B & C) pattern contrast stimulation. The top most waveforms were recorded to the first of the pair presented alone.

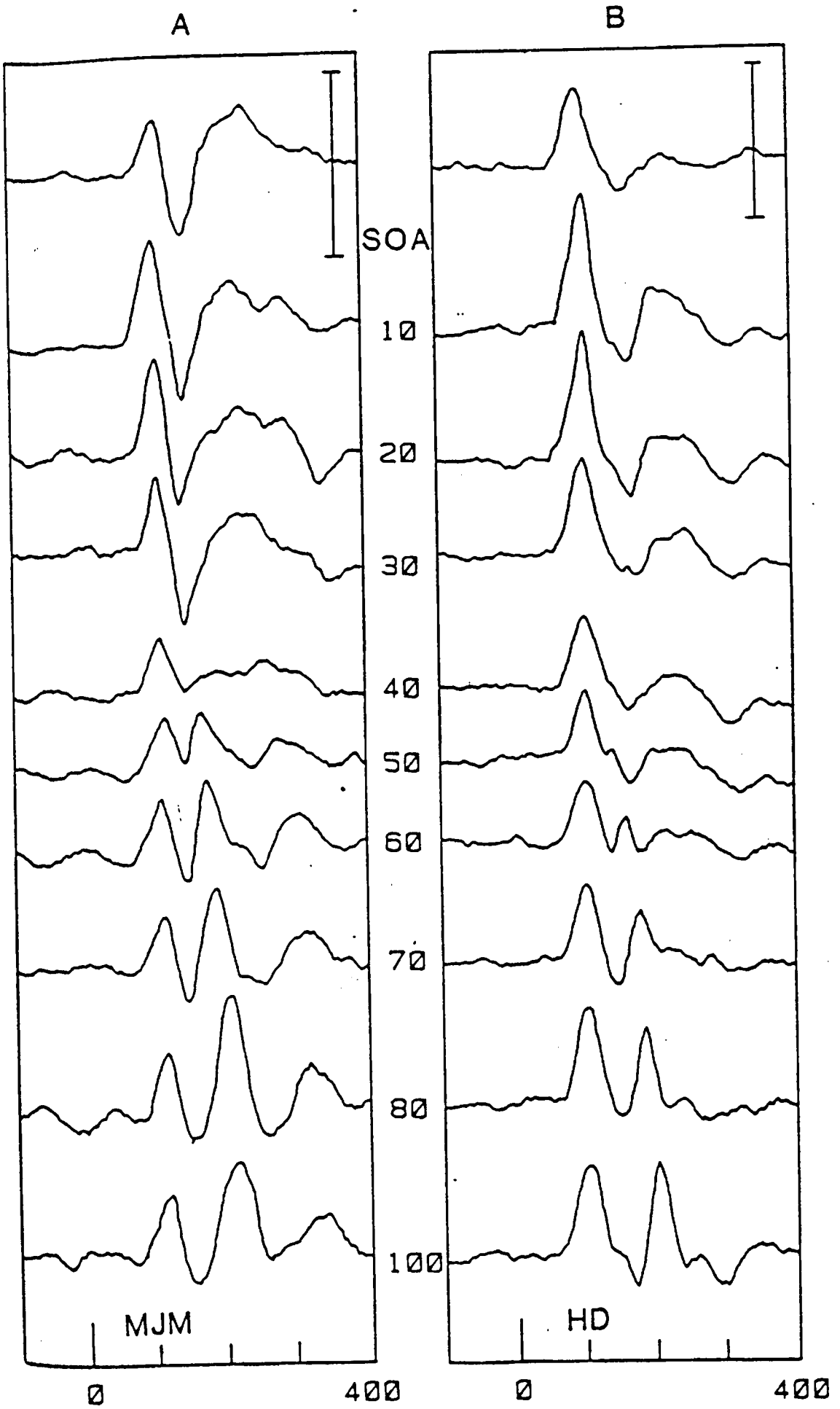


Figure 4.3

As for figure 4.2 but with positive-positive stimulation for subject H.D. and negative-negative stimulation for M.J.M. Stimulus duration was 10 msec. Adaptation level was 2.5 log units lower than used in figure 4.2 (see text for details).

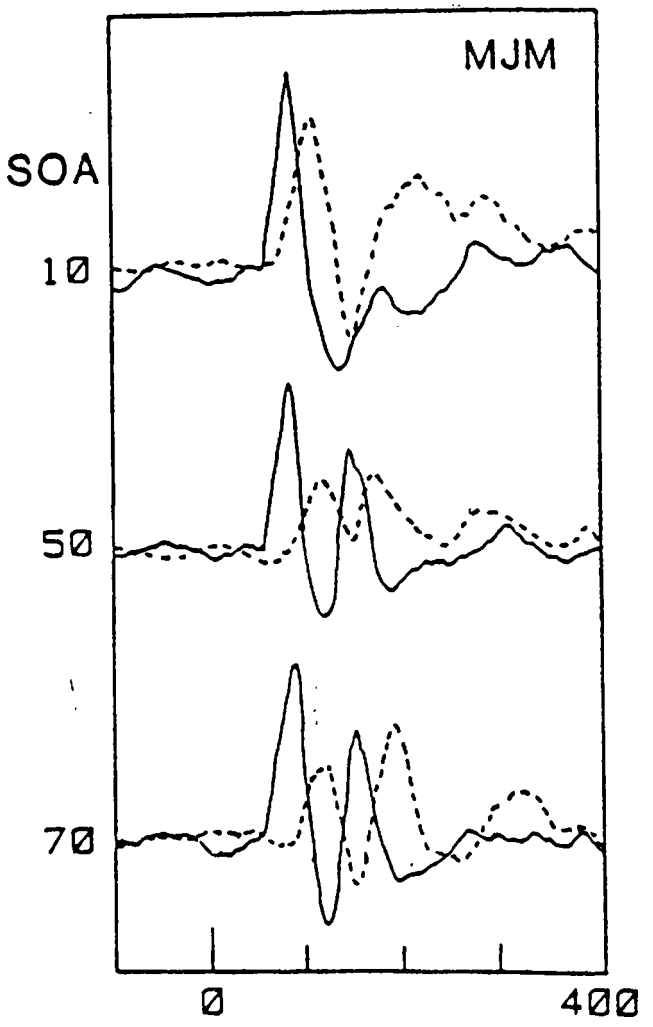
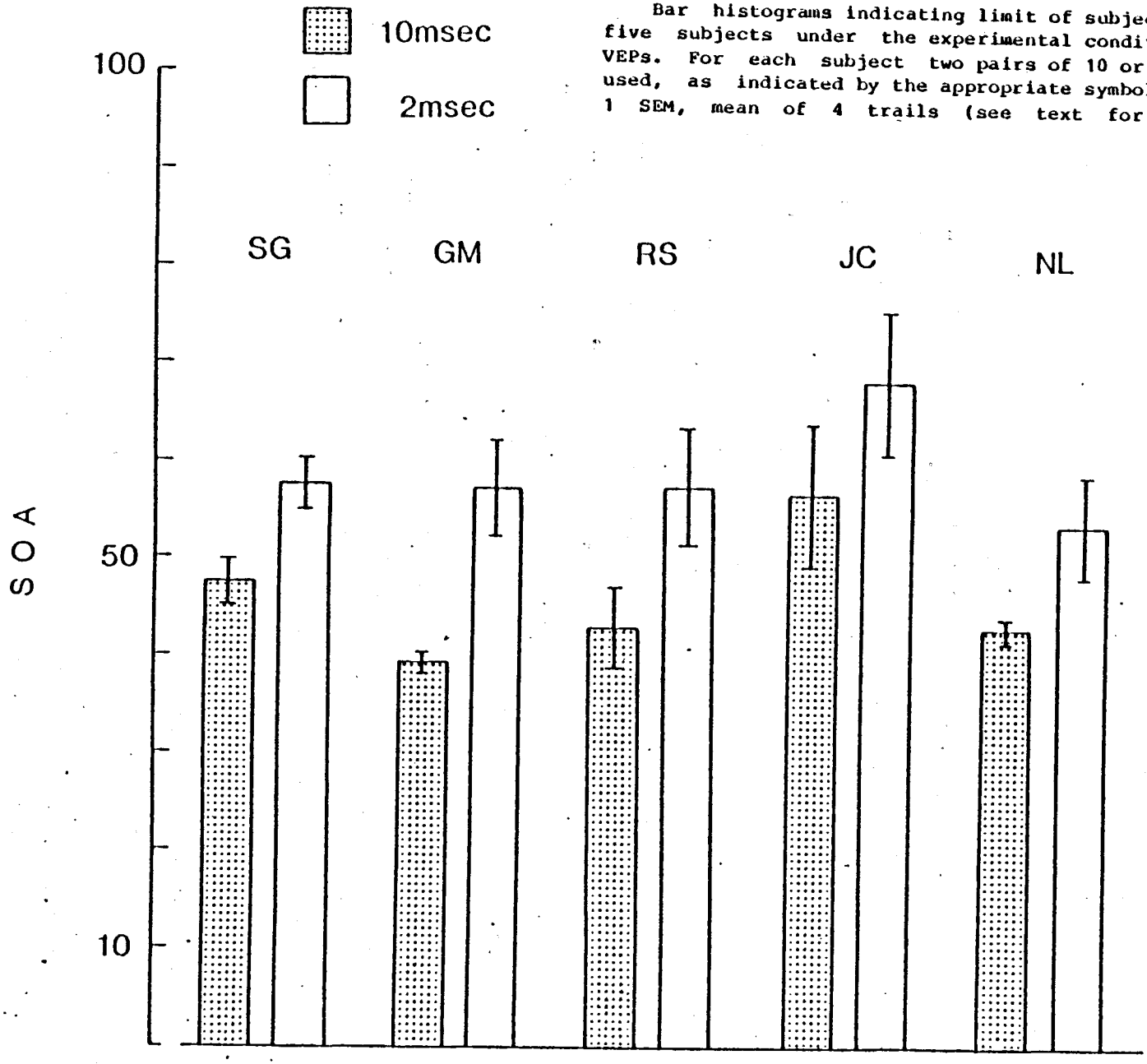


Figure 4.4

Superimposed waveforms at high (full trace) and low (dashed trace) adaptation levels. Indicating increased latency and decreased amplitude of the VEP at lower adaptation levels.

Figure 4.5



Bar histograms indicating limit of subjective resolution for five subjects under the experimental conditions used to record VEPs. For each subject two pairs of 10 or 2 msec stimuli were used, as indicated by the appropriate symbols. Bars indicate +- 1 SEM, mean of 4 trails (see text for details).

whilst for the 2 msec stimuli (which are in fact approximately twice SOA, the duration threshold), the limit lies between 50-60 msec. The value is thus similar to that obtained for the CI component although the slight increase in the subjective limit observed with the 2 msec stimulus found for all subjects, is not evident in the VEP waveforms (see figure 4.7). However it is possible that the increase may be a reflection of the fact that, as subjective contrast is reduced, there is an increase in double pulse 'detection criterion'. This would imply that the limit of neural resolution could remain invariant with regard to the subjective contrast of the patterns (as indeed the VEP data suggest) but that the cut off level of the threshold detector judging the independence of two discrete visual events has been elevated. There is after all a strong likelihood that the level of any such threshold detector of a given stimulus attribute may be biased by cognitive factors, eg 'stimulus set' which may modify, in a 'top down' fashion the threshold level.

4.8:- Temporal Summation. ' Results

One interesting aspect of the data can be observed from a comparison of the waveforms presented in figure 4.2 and 4.3 for the 10 msec duration stimulus presented at both high and low adaptation levels. It is evident that the amplitude of the potential obtained at high adaptation levels shows little sign of summation at the shortest SOA value of 10 msec. This contrasts with the complete summation observed at this onset interval for the low adaptation level. Moreover, for the range of SOAs between 40-70 msec, the response to the first of the pair is of smaller amplitude than that obtained to a single pattern presentation, even though in this range the response to the second of the pair is clearly identifiable.

The summarised data for both positive and negative pattern pairs as a function of SOA for each of the three subjects is presented in figure 4.6. Here, the amplitude of the single peak for values of SOAs less than the critical duration for temporal resolution or that of the first peak for intervals greater than this, are plotted as a percentage of the amplitude of the VEP for a single pattern presentation of the appropriate duration. The non-linear effects evident in the VEP waveforms are more apparent since there is only very slight summation at the shortest SOA for the 10 msec duration stimuli of both contrast polarities presented at the high adaptation level. Reducing the background illuminance by some 2.5 log units increases the amount of

Figure 4.6

Potential amplitude plotted as a function of SOA for both positive-positive and negative-negative conditions.
(▲)= 10 msec duration stimulus at 500 cdm^{-2}.
(■)= 2.5 msec duration stimulus at 500 cdm^{-2}.
(●)= 10 msec duration stimulus at 2.5 cdm^{-2}.
The value of 0 on the summation scale indicates that the peak of the VEP less than the limit of resolution, or the peak of the first VEP for SOA greater than this, is equal to the amplitude of the VEP elicited by a single stimulus.

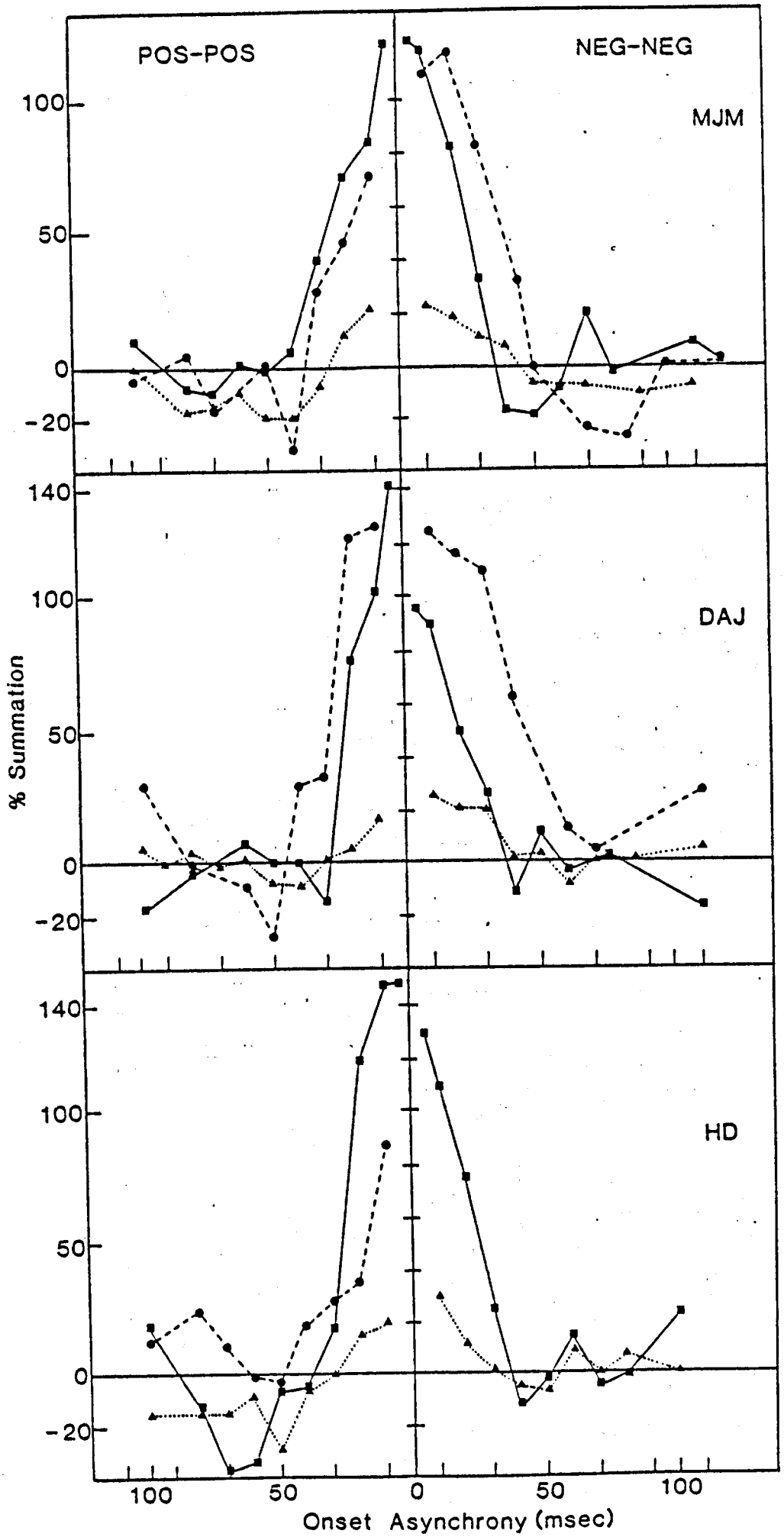
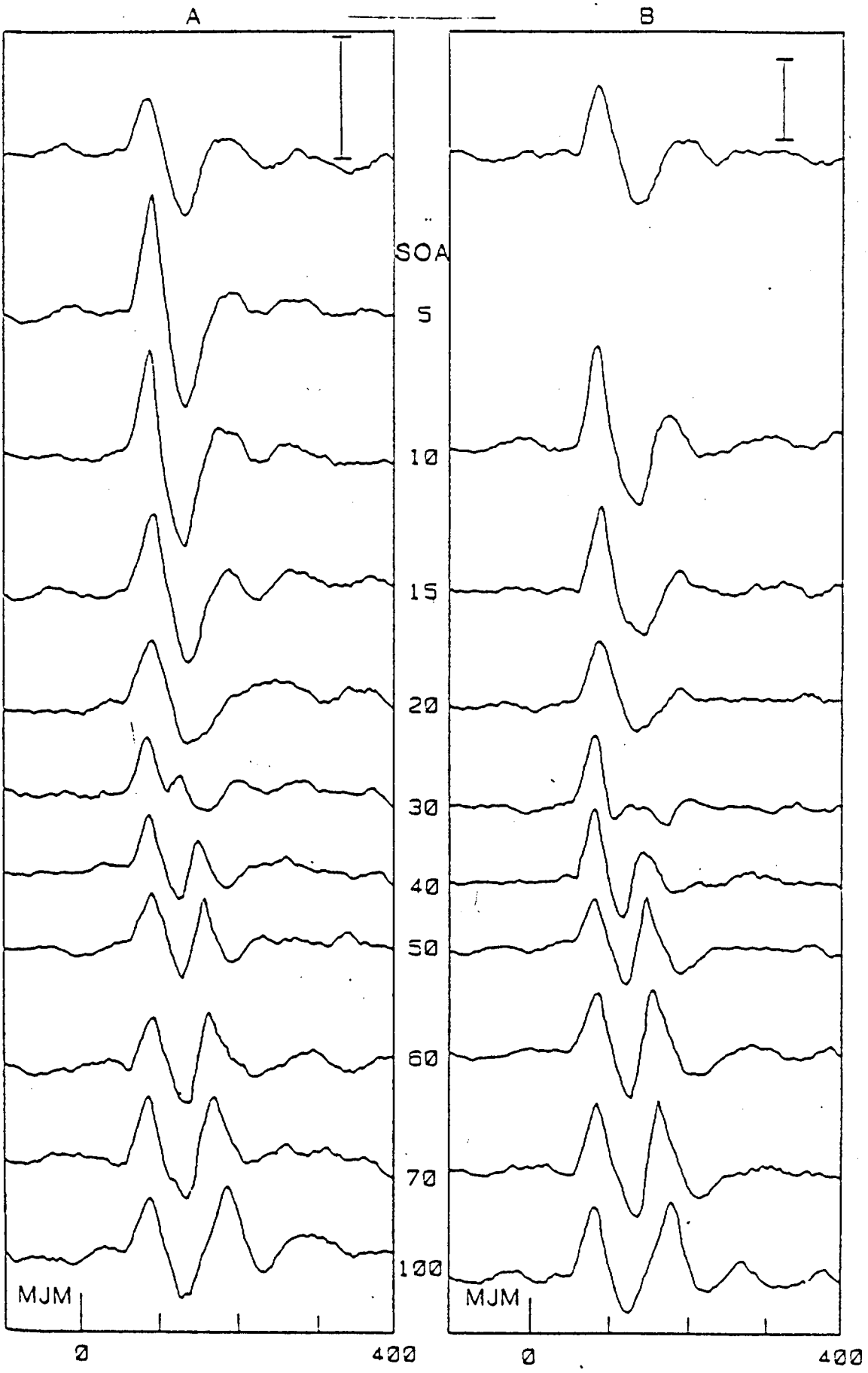

POS-POS
NEG-NEG
MJM
DAJ
HD
100
50
0
-20
140
100
50
0
-20
140
100
50
0
-20
% Summation
100
50
0
50
100
Onset Asynchrony (msec)

Figure 4.7



Waveforms in column A recorded to a 2.5 msec stimulus, 1 msec above subjective threshold. These waveforms indicate the invariance of limiting resolution with stimulus duration (subjective contrast) but suggest increased summation at short SOAs (see text for details).

summation at the shortest SOA, indeed summation is complete at SOAs of between 10-15 msec.

The lack of summation at the higher adaptation level was perhaps surprising given the very linear properties of the component amplitude function obtained in response to single stimuli with constant (contrast/duration) products reported in chapter 3. Moreover the finding that adaptation level influences the extent of temporal summation is contrary to the findings that the limit of both temporal integration and resolution are independent of this variable at least over the range examined. The result is perhaps less surprising, however, if the following fact is considered. As adaptation level is reduced, duration thresholds are raised from appoximately 1-1.5 msec at 500, cdm^2 to 6-7 msec for an adaptation level of 2.5 cdm^2. Thus, in consequence, a stimulus of 10 msec duration would in the former case be approximately seven times the duration threshold whilst in the latter case it would be only twice the threshold value.

If the above argument is correct, then stimuli of 2.5-3 msec duration presented at the highest adaptation level would be expected to produce VEPs whose amplitude functions should show complete summation at the shortest SOAs. If such were the case then it would appear that complete temporal summation is an essentially threshold phenomena. To test this prediction the presentation time of the stimulus presented at the high adaptation level was reduced to 2.5 or 3 msec. From the data presented in figure 4.7, which show the waveforms elicited in two subjects under these conditions, it is evident that the prediction has been borne out. Complete summation for all subjects under each stimulus condition is obtained only for SOAs of approximately 5-15 msec with the slope of the summation curve falling off rapidly to a point at between 40-70 msec SOA where negative values are obtained; this suggests some form of inhibitory interaction between the two temporally independent stimuli.

4.9:- General Discussion

Temporal resolution

I shall firstly consider the question of temporal resolution, defined here as the SOA at which the VEP elicited by the second stimulus separates from that to the first as evident by a well defined

peak in the waveform at a predicted latency from stimulus onset. It may of course be arbitrary as to what aspect of the potential should be measured in this situation. (We do not after all know the exact relationship between VEP amplitude and underlying neural activity). A strict criterion for measuring limiting resolution might be the interval at which the amplitude of the VEP to the second of the pair reaches a value equivalent to that of the first, since it could be argued that at such a point the cortical mechanisms producing these potentials are responding to patterns in an equivalent manner (if the amplitude of the VEP can be considered as a measure of equivalence).

However as will be shown below, the subjective limit of resolution is based on the minimal criterion for contrast modulation detection. It is therefore more reasonable in this case to consider the occurrence of the second response in preference to its actual amplitude. [A careful consideration of the waveforms shown in figures 4.2 to 4.3 suggests that such a procedure is the most physiologically meaningful, in the sense that as the onset interval is increased beyond the limit of resolution, the amplitude of the response systematicaly increases as indeed does the subjective impression of the distinctness and clarity of the second stimulus: a feature which further suggests a close relationship between the properties of this component and sensation]. According to the criteria used therefore the limit of component resolution was approximately 40-50 msec. This value being independent of both adaptation level (over the range used) and stimulus duration.

Temporal resolution is therefore more clearly defined in these experiments than by comparing the responses to single stimuli with constant (contrast/duration) products reported in chapter 3. Such a finding is consistent with the results of Levick & Zacks (1970) for cat retinal ganglion cells. They reported experiments conducted at scotopic background levels, which have shown an integration time constant of approximately 60 msec, the limit of temporal resolution for the same cells stimulated with brief (2 msec) pairs of light spots projected to the centre of the receptive field was some 40 msec SOA. A similar limit of temporal resolution has been reported by Schiller (1968) for units in the layer A of the cat LGN the stimuli in this case again being brief (10 msec duration) pairs presented to the centre of the receptive field.

The limit of VEP resolution (40-50 msec SOA) is similar to that obtained in the psychophysical experiments under the same stimulus

conditions, this value corresponding to that of 53.68 msec SOA obtained when the data of Mahneke (1958) are replotted as a function of stimulus onset interval rather than inter stimulus interval (see Boynton,1973). An equivalent limit would also be obtained if the mean value of a group of normals (used as a control group in a study of subjects with visual disfunction) reported by Galvin and Regan (1976) were to be plotted in terms of the SOA rather then ISI. The mean value of the group being some 50 msec SOA for brief (10 msec stimuli) presented some 3 degrees from the fixation point.

The reasons for plotting limiting resolution in terms of SOA rather than ISI are discussed in more detail in section 4.11.

There has been much debate about the most meaningful criteria on which subjects base their judgement of 'twoness' since it has been suggested by Kietzman (1968) that its determinants are to some extent dependent apon factors which may be defined as 'stimulus set'. In the present experiments, subjects were instructed only to report a single or double presentation and were given no instruction as to what features they might use to distingish the two. Post experimental questioning revealed however that each had in the main used what Kietzman (1967) has called the 'flick' criteria. That is although the subject felt unable to distinguish a distinct 'off' period between successive presentations, they were able to perceive a "shimmering" effect which was interpreted as a double presentation. This is clearly a low criterion response measure and may be based on the activity of cortical mechanisms other then those used in pattern recognition per se.

The notion of two distinct thresholds, one for contrast detection and the other for movement detection in the absence of pattern discrimination has been proposed by a number of workers and supported by the data of Kulikowski (1978). Although Derrington & Henning (1981) suggest that the distinction between these two thresholds may not be so clear as has been suggested by Breitmeyer (1979) since they find that the threshold for the detection of movement, or more appropriately, temporal modulation is dependent upon the discrimination of spatial contrast and thus contrast thresholds. It cannot be denied however that it is easier to detect the occurrence of temporal discontinuity than it is to determine any spatial discontinuity arising from it. It is in this sense that it is suggested that the limit of subjective resolution may be based on mechanisms not directly involved in detailed pattern discrimination.

In conclusion therefore the results of these experiments have shown that, for the stimulus used the limit of neural resolution in the human visual system for brief pairs of contrast patterns is slightly better than 50 msec. In addition this limiting value has been shown to be independent of :-

a-: stimulus duration, below at least 10 msec,

b-: the contrast sign of the stimulus,

c-: the background luminance on which it is presented,

at least over the 2.5 log unit range used here.

The temporal properties of CI are therefore consistent with both single unit and psychophysical estimates of limiting resolution, and reflect the best that the system can do to resolve the particular stimulus pair used. It is suggested that the properites of CI and the psychophysical judgements are ultimately determined by the properties of the same cortical processes.

4.10:- Temporal summation

The data relating to the temporal summation of contrast patterns are more interesting because they provide electrophysiological evidence of a distinct non-linearity in the visual system's response to temporally modulated stimuli. That complete summation should occur only at SOAs of 5-20 msec and only for stimuli which were close to threshold duration is consistent with both neurophysiological and psychophysical data. For example Levick & Zacks (1970) found little evidence of spike summation for cat retinal ganglion cells in response to brief (2 msec) stimuli when at the shortest SOA the combination would be only four times the unit threshold. Schiller (1968), recording from the LGN of cat, reported that complete temporal summation, as measured by percentage response amplitude, was obtained only when the intensity of the stimuli was 0.5 log unit above unit threshold. He further found that when the intensity of the second of the pair was increased to 3.0 log units above threshold summation did not occur even at the shortest onset interval. Indeed, for the low intensity pair, complete temporal summation occurred only at SOAs of 10-20 msec (stimulus duration being 10 msec). Grusser & Kapp (1958) have also reported comparable summation effects at the retinal level to brief pairs of same intensity stimuli.

The properties of CI are therefore consistent with those observed at the single unit level under similar conditions.

There have been extensive psychophysical studies of temporal summation and although direct comparison between the results of these studies and the present VEP data is difficult, because of procedural differences, there are some interesting similarities. Firstly, it of been consistently reported that the interval over which pairs of brief threshold stimuli produce complete summation is significantly shorter than the critical duration for which Bloch's law will hold for single stimuli. A number of studies (Battersby,1970; Blackwell,1963; Grossberg,1970; Ikeda,1965; Rashbass,1970) have reported complete threshold summation only when the onset interval between stimuli was small; the actual values being between 10-20 msec (for stimuli that have ranged, in angular subtense from 30'arc to 17 degrees of visual angle). These results are similar to the present data for the CI component, although Ikeda's (1965) study is the only one to have reported on both positive- and negative-going pulses (see figure 4.8).

Apart from finding complete threshold summation only at short intervals, the above studies have also reported that for SOAs between 40-80 msec negative summation is observed whereby the threshold for the pair is higher than that for a single stimulus. This effect is illustrated in the figure 4.8 from Ikeda's study. For onset intervals greater than approximately 70 msec, a slight elevation of threshold is obtained, which likely is to be the result of probability summation. However, the increase in threshold observed at intervals of 40-70 msec has led to the suggestion that over this range some form of inhibitory interaction occurs between the temporally independent stimuli which, Ikeda's study suggested is found only when each member of the pair is of the same threshold intensity and duration.

Baumgardt & Segal (1942) have reported a similar phenomenon at supra-threshold levels. As is evident in figure 4.6, the slope of the amplitude function for CI also becomes negative over this range, although it should be noted that there is some degree of variability between subjects as to the extent and time course of the effect. This variability may imply that the effect is not a real one in the sense of reflecting underlying neural activity and may for example have merely resulted from the temporal overlap of succeeding potentials recorded from the same electrodes; the response to the second stimulus dragging down that to the first. Whilst this appears to be the likely explanation, it is possible that the decrease in amplitude could reflect some underlying neural interaction. The evidence to support

this suggestion comes from a series of experiments to be reported in chapters 7 and 8 on the phenomena of visual pattern masking and metacontrast.

The interactions observed in the experiments of this chapter are dependent upon the spatial superimposition of the contrast elements of the patterns. Whilst the 'inhibitory' effect may not be determined by the same mechanisms or indeed be equivalent to that observed psychophysically the evidence does suggest that it reflects some form of neural interaction which may occur at levels distal to the site of the VEP generator. It is interesting to note that the 'inhibitory' effect is observed at SOAs close to the critical duration for single stimuli with constant (contrast/duration) products reported in chapter 3. A similar relationship has also been noted by Roufs (1973) and Rashbass (1970) in regard to their psychophysical data, and has led the latter to suggest that a single mechanism may be determining the two functions. Several models have been proposed to account for these effects, see for example Roufs (1974) and Rashbass (1976). Such models have, each in their turn, stressed either photochemical or neuro-retinal processes as being critical in determining the temporally dependent functions. Battersby (1970) has however argued that either explanation, taken alone, has difficulties in explaining all the relevant data and has suggested that central factors may need to be considered. The extent to which this will be the case is of course likely to depend on experimental conditions.

The limited neurophysiological data discussed above, has shown that at levels prior to that at which any but weak binocular interaction is observed, temporal summation as measured by discharge amplitude show similar non-linear properties to that observed psychophysically; this suggests that the mechanisms that determine these functions are situated at relatively low levels which would of course be consistent with either a photochemical or neuro-retinal explaination.

Breitmeyer & Ganz (1977), have investigated threshold summation for pairs of sine wave gratings of variable spatial frequency. They report that complete summation for both high and low spatial frequencies occurs only at SOAs of less than 20 msec. They also report negative summation at and around 40-70 msec SOA similar to that observed for both the VEP data and that reported by other workers for simple spot stimuli.

Watson & Nachmias (1977) in a more detailed study have also reported spatial frequency dependent threshold summation. The most interesting aspect of their data is the finding that whereas for low frequency gratings, there is a range of temporal intervals which produce inhibition between same-phase pairs and facilitation for opposite phase pairs similar to the phenomena reported by Ikeda (1965); no such effects are observed for spatial frequencies higher than 7 cpd, as shown in figure 4.9. The time course of positive summation for same-phase pairs of differing frequency was very similar, the major difference being the absence of the inhibitory effect evident over the temporal range 30-70 msec for low spatial frequencies. These authors account for their data in terms of a model similar to that of Rashbass (1976) in which a detector operates on the squared, integrated output of a linear temporal filter. Because negative summation is not observed for high frequency gratings they suggest that the underlying spatial temporal filters have 'sustained' properties, that is, they respond in a sustained manner. When spatial frequency is progressively reduced the properties of the spatio temporal filters thus revealed become primarily transient. However the time course of summation for high spatial frequencies was only some 20-30 msec longer than that of the lowest frequency.

A similar effect has been reported by Meijer et al (1978) who examined temporal summation as a function of stimulus size. They report that the negative dip in the summation curve is only obtained for dots of medium to large angular subtense, for dots smaller than about 11'arc there is no negative summation but a progressive increase in dot size produces a systematic increase in negative summation at onset intervals of about 40-70 msec. They however report that there is no comparable size-dependent interactions for stimulus pairs of opposite contrast sign, (doublets). Thus although their data shows similar size dependent summation curves for same sign stimuli to those reported by Watson & Nachmias (1977), their data for opposite-sign pairs is not entirely consistent with the notion of sustained and transient spatio temporal filters.

However, the temporal summation curves for contrast gratings are similar to that observed for CI which suggests that psychophysical and electrophysiological data are in quantitative agreement, implying that the time course of temporal summation observed psychophysically is determined by neural mechanisms at or prior to the striate cortex.

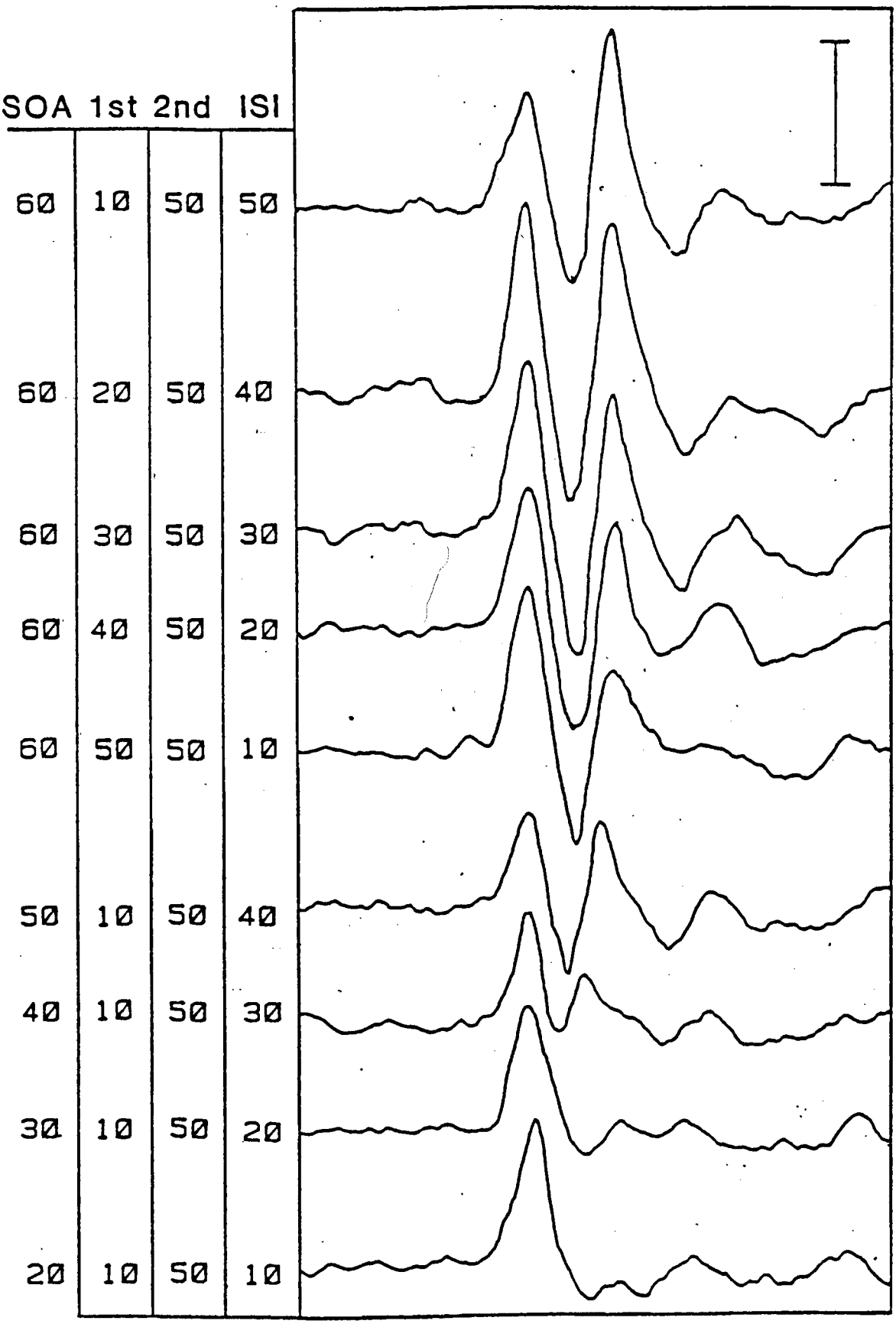


Figure 4.9

VEPs to stimulus pairs at constant SOA (waveforms 1 to 5, from top) and constant inter-stimulus interval. ISI is reduced by increasing the duration of the first stimulus in the pair.

The four waveforms at the bottom of figure are recorded when the inter-stimulus interval, and stimulus duration is held constant and the SOA progressively decreased.

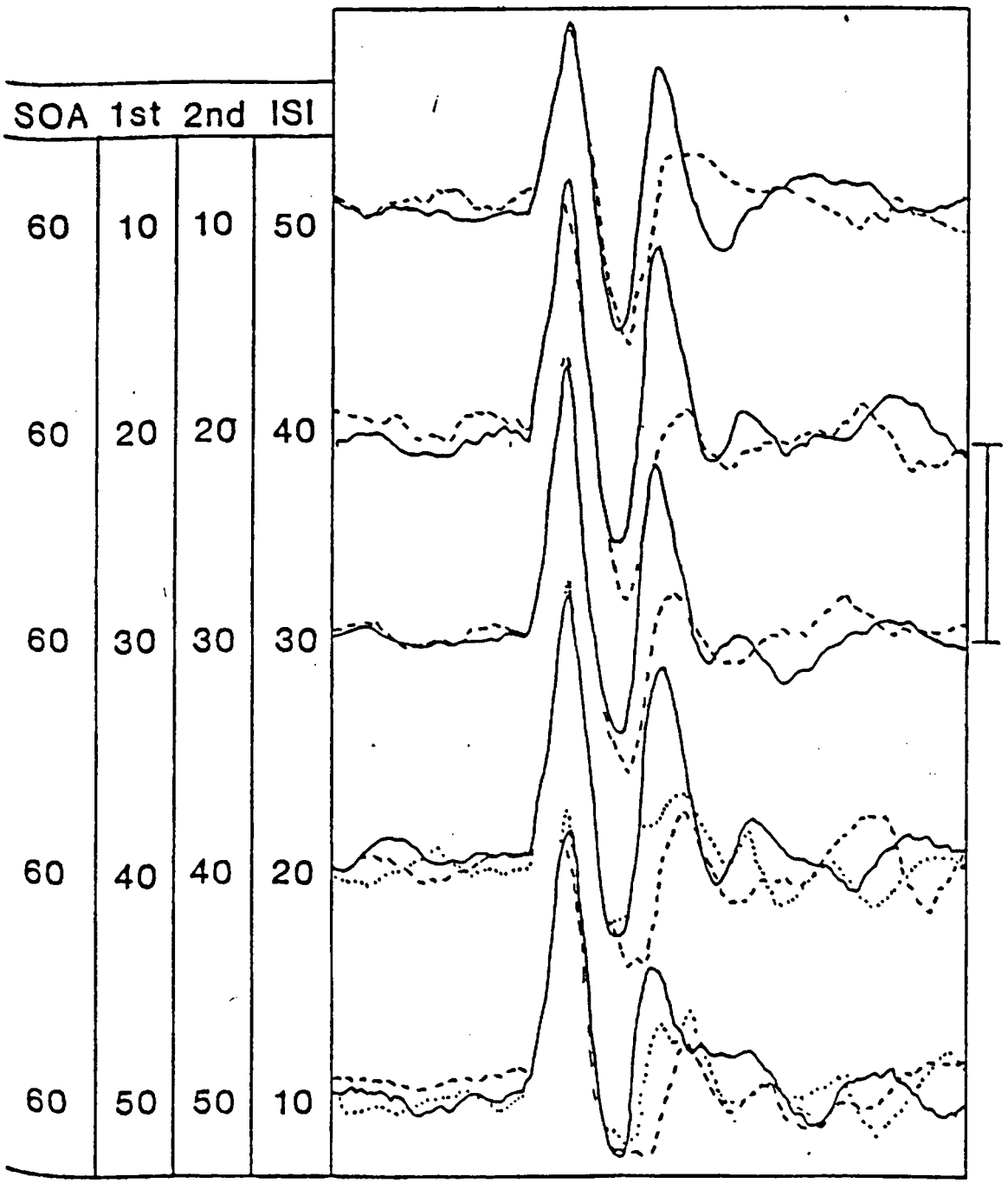


Figure 4.10

VEPs elicited when SOA and stimulus duration are held constant and inter-stimulus is progressively reduced. The full traces are the VEPs elicited by pairs of stimuli. The dashed traces recorded to the first of the pair presented alone, and the dotted trace recorded to a single stimulus equivalent in duration to the sum of the stimulus duration and the inter-stimulus interval.

4.11:- Does SOA or ISI determine limiting resolution

A question of some importance in measuring the critical interval for temporal resolution is the adoption of a meaningful measure between the occurrence of the two temporally independent stimuli. In the preceding experiments, and indeed in subsequent ones the chosen metric has been the onset interval. No justification has as yet been given for the use of this criterion either on theoretical or experimental grounds. In the following experiments an attempt is made to determine which is the most physiologically appropriate measure.

Consider the following situation. Two brief pulses of 1 msec duration are presented and the interval between them varied. It is found that subjects judge the two events as independent at ISI of 60 msec. Both stimuli are then increased in duration from 1 to 40 msec and the interval between them again varied. The subject now reports that the two events appear independent at an ISI of 20 msec. One conclusion which could be drawn from this result is that temporal resolution improves as stimulus duration is increased, indeed this is the conclusion reached by Mahneke (1958) in a detailed study of the effects of stimulus duration and ISI as determinants of temporal resolution.

However one might, as Boynton (1973) has done, replot Mahneke's data in terms of the onset interval and find that the limit of resolution, of some 55 msec SOA, is in fact independent of both stimulus duration and ISI, at least for stimuli whose durations are below the limit of resolution obtained with brief stimuli. The implications of this difference is important, particularly as these psychophysical data are often interpreted in terms of underlying physiological processes. Unfortunately there has to my knowledge been no attempt to settle the dispute as to the most meaningful measure of temporal resolution by obtaining electrophysiological data obtained under psychophysical conditions.

Methods

The stimulus pattern used in these experiments was the regular dot pattern of positive contrast. The CI component was again recorded under standard conditions. The procedure was as follows. Responses were

obtained to brief pairs of patterns as a function of increasing SOA up to the point of complete component resolution. The onset interval was then held constant and the duration of the first stimulus increased progressively to the point at which it had an duration equivalent to the onset interval for complete component resolution.

Results and Discussion

In figure 4.9 are shown typical waveforms recorded when SOA was constant and the duration of the first stimulus varied between 10-50 msec. The duration of the second stimulus was constant at 50 msec. It is clear that component resolution is little affected by such a manipulation. In figure 4.11 are also shown the waveforms obtained when SOA was held constant and the duration of both stimuli increased from 10-50 msec. This has the effect of reducing ISI from 50 to 10 msec. Again, however the limit of resolution remains constant, although there appears to be some reduction in the amplitude of the potential evoked by the second stimulus of the pair.

In figure 4.9 are shown the waveforms obtained when both ISI and SOA are systematically reduced from an onset interval of 50 msec to that of 10 msec. It is clear that in this condition the response to the second stimulus is progressively reduced, the extent of this effect being dependent on the SOA, since a comparison between the waveform obtained at the 10 msec ISI condition (60 msec SOA) shows that the response to the second stimulus is of far greater amplitude that than obtained at 30 msec ISI (30 msec SOA). This result cannot be due to any saturation effect the first stimulus may have on the response to the second because at 10 msec ISI (60 msec SOA) the duration of the first stimulus was 50 msec which at this level of stimulus contrast is in fact above saturation level. The response to the second of the pair was clearly evident.

When the duration of the first stimulus of the pair approached the critical SOA for complete temporal resolution the amplitude of the VEP elicited by the second of the pair was gradually attenuated. Compare for example the responses obtained at ISI's of 50 msec (stimulus duration 10 msec) with that of the waveform obtained a ISI's of 10 msec (SOA 60 msec). This suggests that the limit of resolution is dependent on ISI or stimulus duration when this exceeds a certain value. A further possible explanation is that the high contrast pattern used in this experiment have caused some saturation within the system.

Discussion

These short experiments have shown conclusively that the factor which limits the neural resolution of brief discrete pairs of patterned stimuli, is the stimulus onset interval. These results justify the use of this metric as a measurement of temporal resolution of the system and is direct electrophysiological evidence supporting Boynton's (1973) predictions.

Chapter 5:- Temporal resolution and summation of opposite contrast pairs (doublets)

Introduction

Psychophysical studies (Ikeda,1965; Rashbass,1970) have shown that over the interval for which brief stimulus pairs of same contrast polarity show complete threshold summation, partial summation, inhibition and finally probability summation, doublets produce cancellation, partial cancellation, potentiation, and probability summation respectively. The slopes of the summation curves obtained under the different conditions appear to be the mirror images of each other, as shown in figure 5.1A, which is taken from Ikeda (1965). The locus and nature of the neural interactions which determine these psychophysical functions are uncertain, although a number of models have been proposed (Roufs,1973; Rashbass,1970; 1976).

To continue the investigation of the temporal properties of CI, the experiments reported in this chapter will examine the time course of temporal summation, and the interval for temporal resolution, of brief doublet patterns. It is hoped that this study will provide a clue as to the physiological basis for the threshold interactions which are observed psychophysically.

5.1. Experiment 5.1:- Temporal summation and resolution of doublets

Procedure

The method of component isolation and stimulus presentation was similar to that of the preceding chapter. In the present case however background luminance was reduced to 136 $cdms^{-2}$. For the first experiment tachistoscope A was used. In the second series dichoptic presentation was achieved by using tachistoscope B. The luminance of the positive contrast pattern elements was again adjusted by each subject, until it had the same duration threshold as the negative contrast pattern. The regular dot pattern was again used.

Three to four runs of 20-25 sweeps were undertaken at each SOA, and both negative-positive and positive-negative combinations were used. Stimulus durations were 10, 5 or 2.5 msec.

Results

In figures 5.2 are presented the waveforms obtained for one subject in response to both positive-negative and negative-positive combinations, where each member of the pair is of 10 msec duration. The waveforms obtained in each of the runs of either 20 or 25 sweeps have been superimposed at each SOA to give an indication of the repeatability of the responses over time. The three to four runs for each SOA were then averaged off line to give the final averaged waveform from which measurements of amplitude and limiting resolution were obtained. Figure 5.4 illustrates waveforms recorded in two subjects to near threshold stimuli of either 2.5 or 3 msec duration.

A comparison between the waveforms shown in these figures indicate two features. Firstly, the extent of potential cancellation observed at short SOAs is dependent upon the duration, and hence subjective contrast, of the two stimuli. At SOAs of 5-10 msec there is complete response cancellation for the case of the short duration stimuli but only partial cancellation is produced for the pairs of 10 msec duration stimuli over the same SOA.

In figure 5.5 the amplitude of the potential evoked by the pair below the limit of resolution, or that of the response to the first stimulus in the pair for durations greater than this (expressed as a percentage of the response evoked by the first of the pair presented in isolation), has been plotted as a function of the SOA. Clearly for pairs of short duration stimuli (2.5 or 3 msec) complete response cancellation is observed at short SOAs for both negative-positive and positive-negative order. The degree of cancellation observed at short SOAs is in fact systematically dependent on the duration of the pair as is shown in figure 5.5 for subject MJM. At onset intervals of around 50 msec the amplitude of the VEP elicited by doublets becomes equal to or greater than that evoked by a single pattern presentation of the appropriate duration. Indeed at these SOAs there is evidence of slight positive summation although its extent is variable. Despite the between-subject variations, the effect would appear to be a real one as it is consistent across conditions.

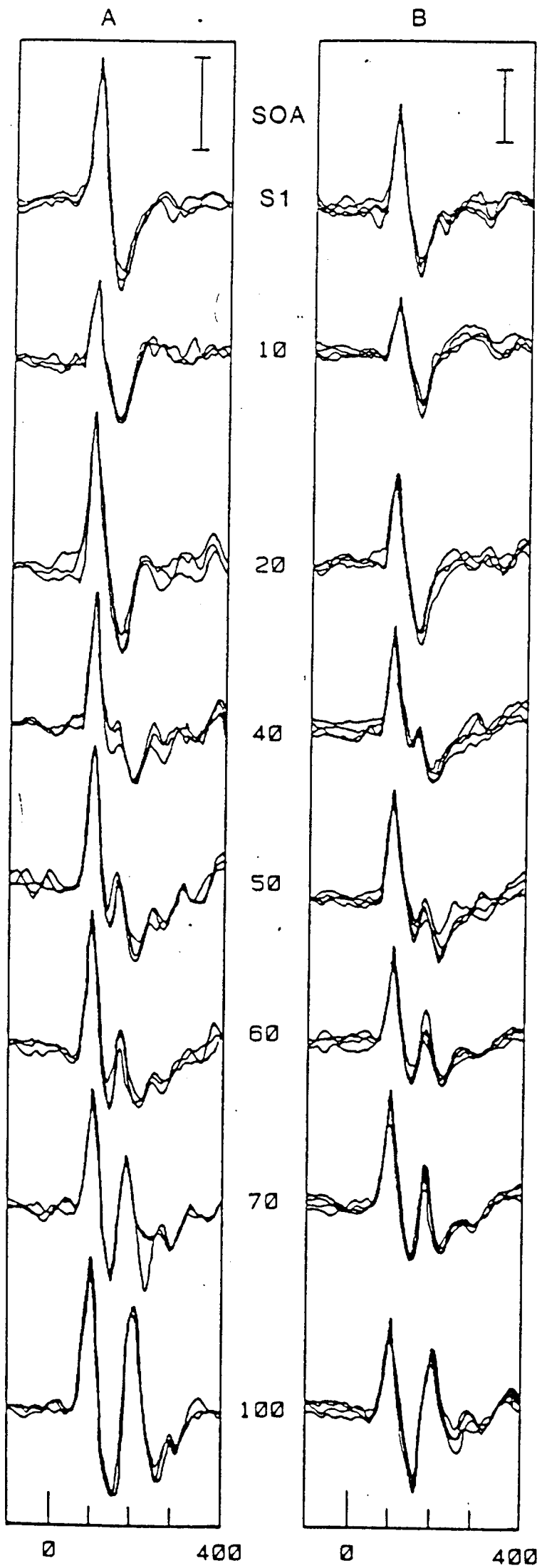
Figure 5.2

Typical form of the VEPs elicited by opposite contrast pairs.

Column A, for positive-negative combination, each waveform represents one run of 25 sweeps, and there are three runs for each condition.

Column B, is for the negative-positive combination each waveform represents one run of twenty sweeps, and there are four runs for each condition.

These waveforms illustrate the repeatability of the responses under both as a function of time and stimulus condition.


A
B
SOA
S1
10
20
40
50
60
70
100
0
400
0
400

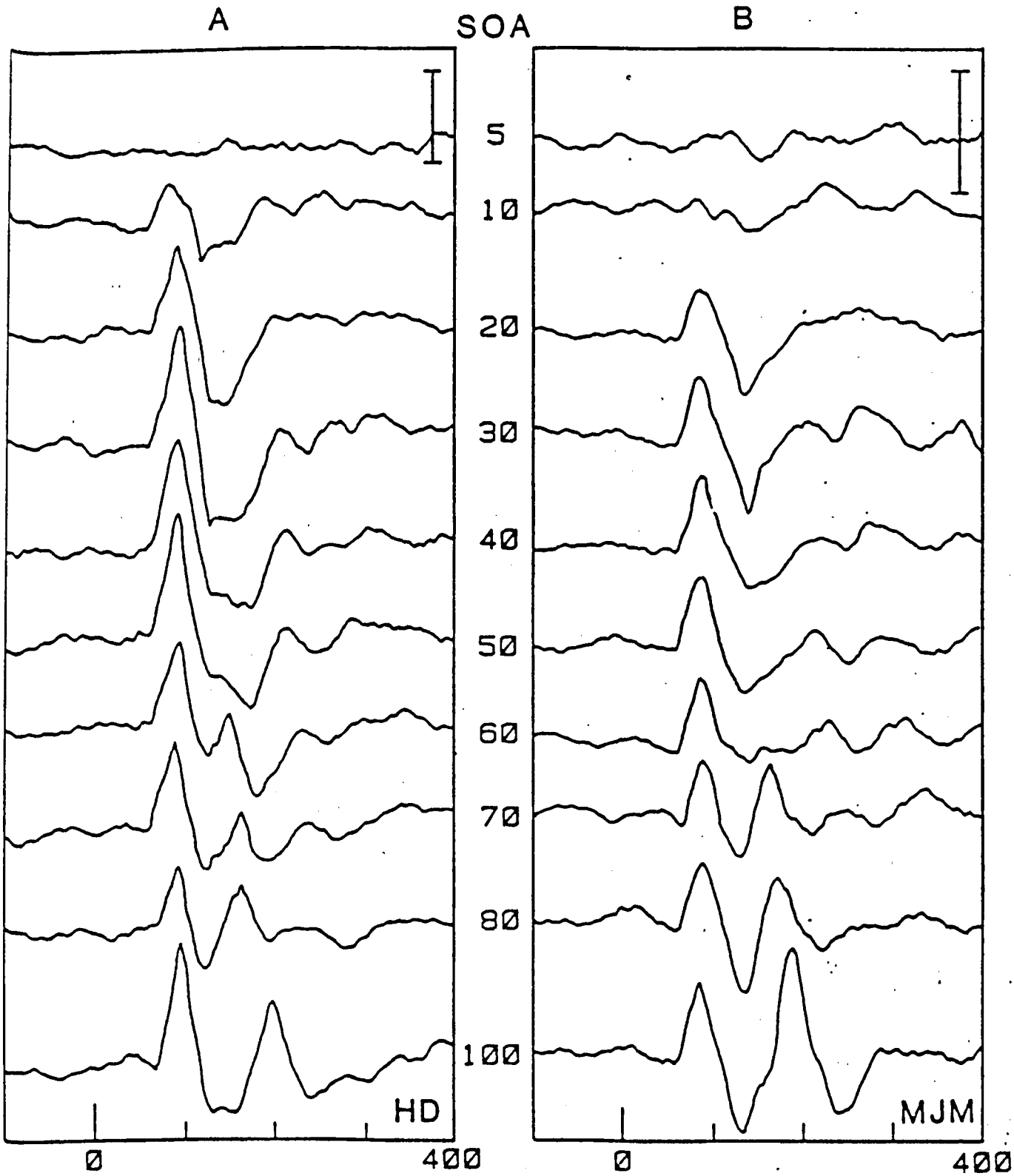


Figure 5.4

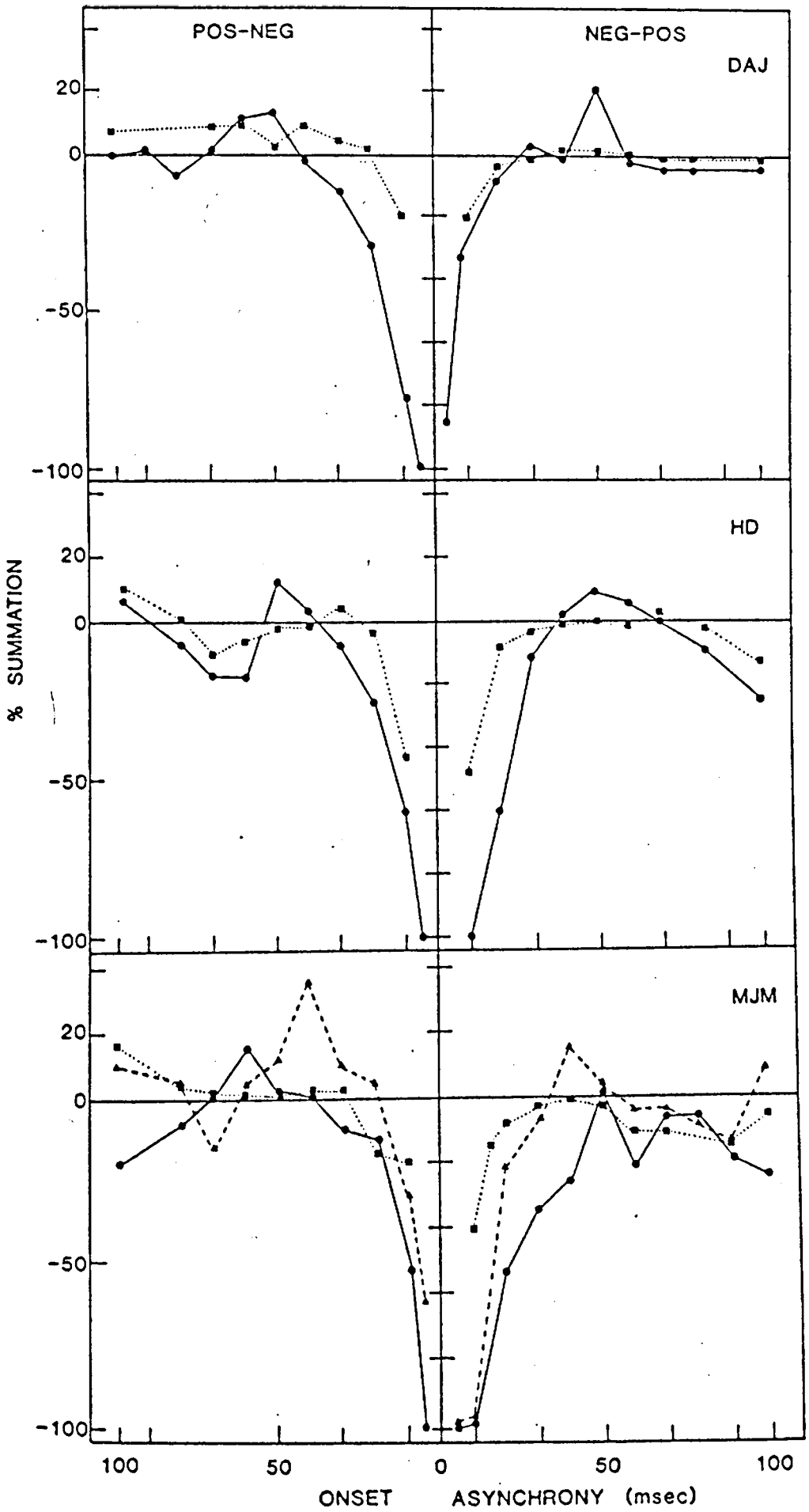
VEPs for two subjects elicited by stimulus pairs of either 2 or 3 msec duration. These stimuli are close to threshold and indicate the fact that as duration is reduced component cancellation increases, becoming complete, at short onset intervals. This being the case for both subjects.

Figure 5.5

Plots of VEP amplitude for three subjects as a function of stimulus onset interval. Here the amplitude of the peak for intervals less than the limit of resolution or the response to the first of the pair for intervals greater than this, as a percentage of the VEP elicited by the first of the pair presented alone.

For subject M.J.M. a more extensive range of stimulus durations have been used which indicate that the extent of component cancellation produced at short SOAs dependent on stimulus duration, and by implication subjective contrast.

The slopes of the summation curve are similar for each subject, with little component cancellation observed at short SOAs for the 10 msec duration stimuli.


POS-NEG
NEG-POS
DAJ
HD
MJM
20
0
-50
-100
% SUMMATION
100
50
0
50
100
ONSET ASYNCHRONY (msec)

There is a further curious effect at and around the values of onset interval which produce the slight summation effect, for it appears from the waveforms of figure 5.4 that limiting resolution is dependent upon stimulus duration. Whilst the 10 msec stimuli of opposite contrast have a similar limit of resolution to that of pairs of the same polarity, temporal resolution for the shorter duration pairs, (2.5 to 3 msec), is some 30 msec longer than that of same-sign pairs of equivalent duration reported in. chapter 4. Although these differences appear real, the experiments were conducted under different conditions and at a later time and it is possible that some varible may not have been controlled for. I decided therefore to compare limiting resolution for doublets with that for pairs of the same contrast sign in the same experiment.

5.2. Experiment 5.2:- Temporal resolution of same and opposite sign contrast patterns.

Procedure

Stimuli and recording conditions were the same as used in experiment 5.1 although in the present case pairs of patterned stimuli of the same contrast polarity and presented at the same adaptation level were also used. This was achieved by using the first stimulus of the doublet and switching it twice during the cycle. Only one subject was used and SOAs were confined to the range between 40-100 msec. Stimulus duration was 10, 5, 3 or 2.5 msec. A negative-positive and negative-negative sequence was used.

Results

In figure 5.6 are shown the waveforms produced by the stimuli used in these experiments. It is clear that for same sign stimuli the limit of resolution is independent of stimulus duration, and thus subjective contrast, and so is consistent with the data reported chapter 4. However, for doublets the onset interval at which the VEP to the second stimulus of the doublet pair is seen is clearly dependent on stimulus duration: being systematically delayed as presentation time is reduced; from from approximately 40 msec SOA at 10 msec duration, to 70-80 msec SOA for stimuli of 3 msec duration.

At the foot of each column are shown the potentials obtained at an SOA of 10 msec for each combination of pattern pairs. Consistent with

Figure 5.6

Typical waveforms recorded in subject M.J.M. under conditions of experiment 5.2.

The three columns illustrate VEPs obtained to doublets of three different duration:-

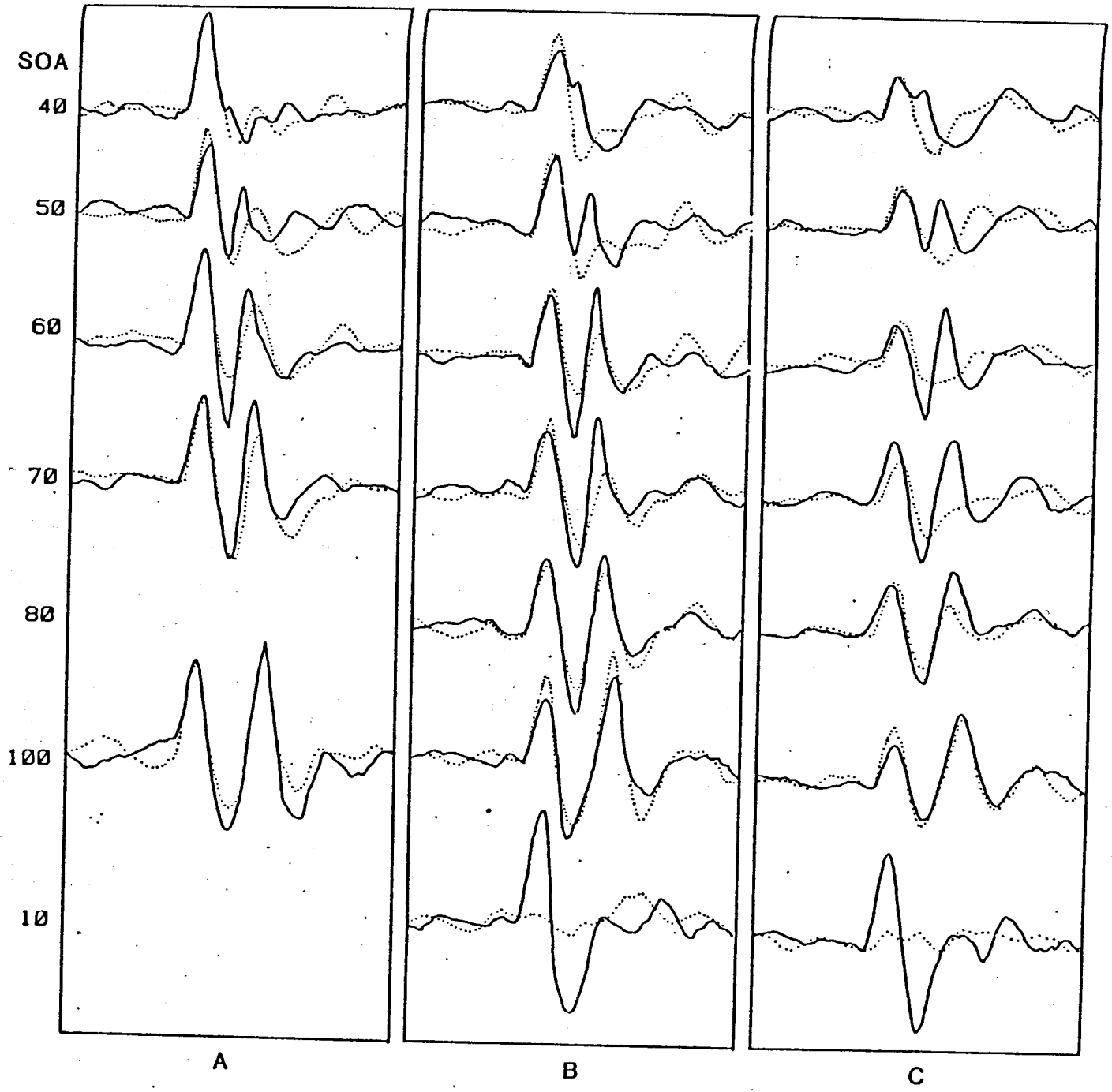
Column A = 10 msec duration
Column B = 5 msec duration
Column C = 3 msec duration.

The continuous traces are for the same contrast sign pairs. The dashed trace for opposite contrast pairs.

At the bottom of each column are shown VEPs recorded at the shortest SOA, indicating as reported above, that opposite contrast pairs produce progressively increasing cancellation at short SOA for short duration stimuli.

For same sign pairs the opposite effect is evident, and VEPs show increased (positive) summation at short SOAs as stimulus duration is reduced.

The limit of resolution for opposite contrast pairs is therefore dependent on stimulus duration.


SOA
40
50
60
70
80
100
10
A
B
C

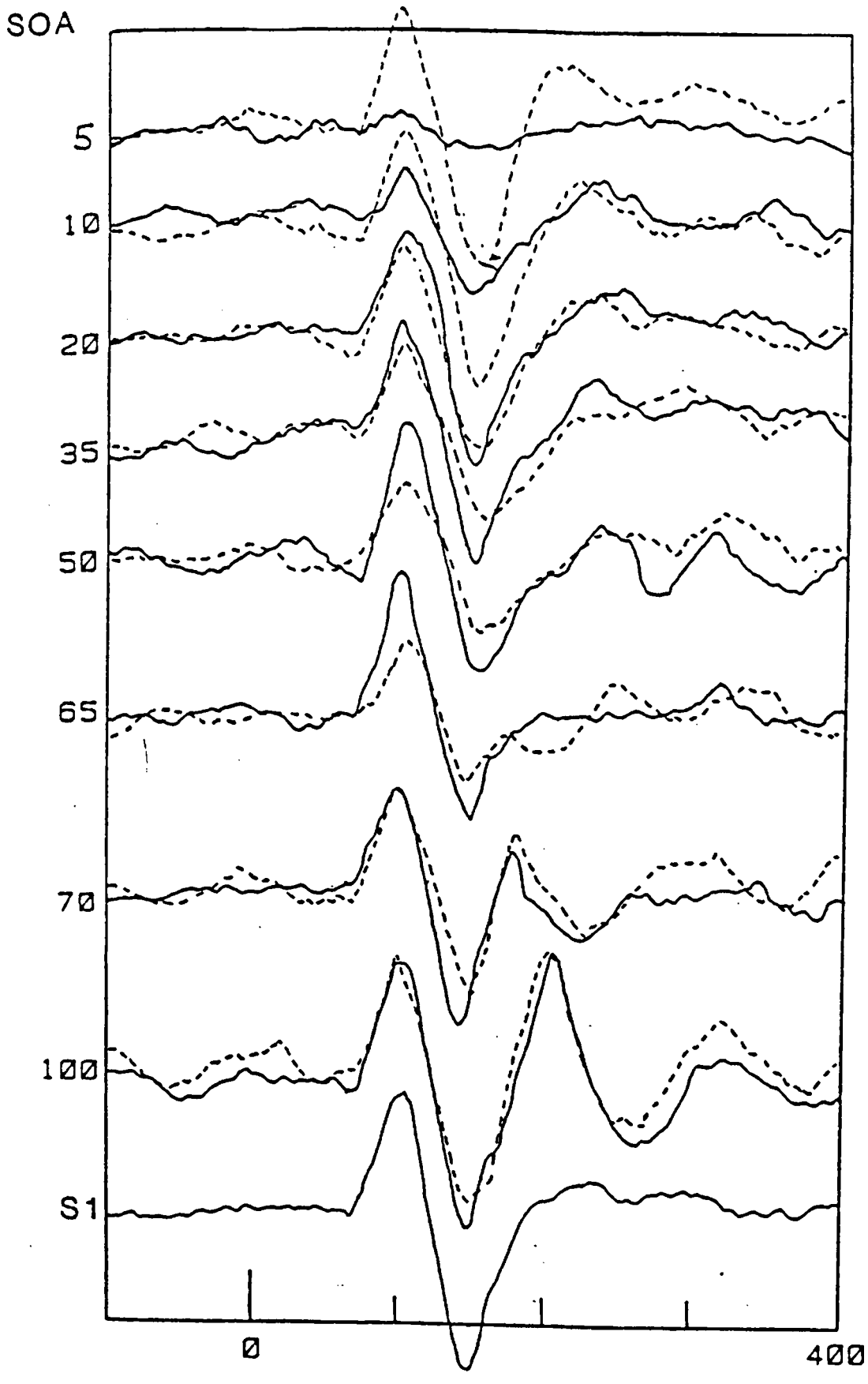


Figure 5.7

Typical form of the response obtained under monoptic (continuous trace) or dichoptic (dashed trace) viewing conditions. Ilustrating that component cancellation is observed only under monoptic conditions.

previous data the degree of response summation, whether positive or negative in nature, is dependent on stimulus duration, being greater for stimuli of very low subjective contrast.

5.3. Experiment 5.3:- Interocular transfer of the negative summation effect

It is probable that the results obtained in experiment 5.1 are the result of interactions occurring at levels distal to the cortex. It is however necessary to check this by comparing the responses obtained to monocular and dichoptic presentation. If response cancellation resulted from some form of cortical interaction then the slope of the summation curve should be similar. If, in contrast, peripheral mechanisms were involved then with dichoptic presentation, positive, rather than negative summation should be evident in the VEP recorded at short SOAs. This effect may be the result of 'real' neural summation within binocular driven units of the striate cortex, which are adequately stimulated by contrast stimuli of either polarity, or would perhaps be more likely to reflect the independent stimulation of monocular units of which there has been reported to be a higher percentage in the striate cortex (Poggio & Fisher,1977).

Procedure

Tachistoscope B was used. The positive pattern presented to the right eye and the negative pattern to the same hemi retina of the left eye. For monocular stimulation the right eye was used. In each case a positive-negative sequence was presented. The stimuli were the same as used in the preceding experiments. Two subjects were used.

Care was taken to properly align these patterns.

Results

In figure 5.7 are presented the waveforms obtained for opposite contrast pairs presented either monocularly or dichoptically. Under the monoptic viewing conditions potential cancellation is evident at short SOAs, consistent with the results obtained for binocular viewing in experiments decribed above. The time course of effective negative summation is also similar to that found previously.

Under dichoptic viewing, however, positive summation is obtained at short SOAs which suggests that the interactions observed under

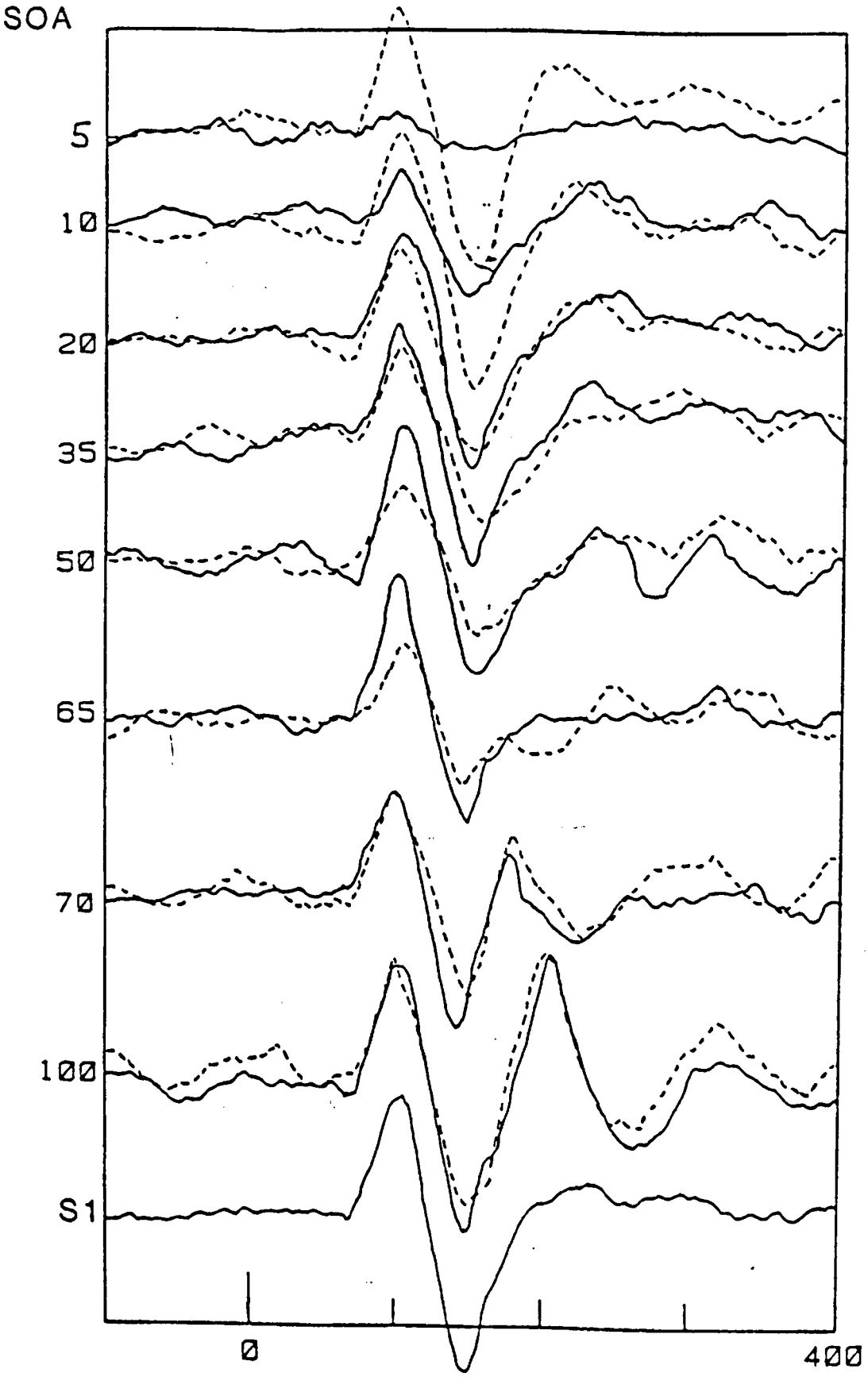


Figure 5.7

Typical form of the response obtained under monoptic (continuous trace) or dichoptic (dashed trace) viewing conditions. Ilustrating that component cancellation is observed only under monoptic conditions.

monocular and binocular viewing are determined by interactions at levels prior to the visual cortex.

5.4. Experiment 5.4:- Effect of spatial non-contiguity on the time course of the negative summation effect

The exact locus of the interactions thus far observed would be difficult to determine by evoked potential studies alone. However, it might be predicted that if non-retinal mechanisms are involved then the effect should be relatively insensitive to the exact spatial contiguity of the pattern elements. A purely retinal mechanism should be sensitive to the relative spatial contiguity of the stimuli and misalignment, however slight, would be expected to abolish potential cancellation.

Misalignment of the two patterns produces a configuration with alternate rows of light and dark dot elements. Presenting such a stimulus briefly with an interval between their onsets is exactly the conditions under which metacontrast masking is observed (see chapter 8). Indeed, with the present configuration, when both stimuli are of the same duration and effective contrast, the first of the pair appears masked for SOAs in the region of 40-90 msec. However some models have suggested that the mechanisms which determine the interactions observed between spatially non-contiguous patterns are primarily of retinal origin (Alpern,1953). The previous results would lead one to predict that cancellation would be observed only for spatially contiguous pairs and so reflect retinal interactions.

Experiment 5.4 set out to test these predictions.

Procedure

One subject was used. Viewing was monocular and the pair were presented for duration of 10, 5, 3 and 2.5 msec to the right eye.In each case SOA was varied randomly in 10 msec steps from 10 msec up to 80 or 100 msec.

Results & Discussion

In figure 5.8 are shown the waveforms obtained for each of the conditions used. As predicted, there is no evidence of cancellation at short SOAs for any stimulus duration. The data indicate therefore that the the interactions observed in experiments 5.1 are probably of a retinal origin as they are abolished by misalignment. Despite the fact

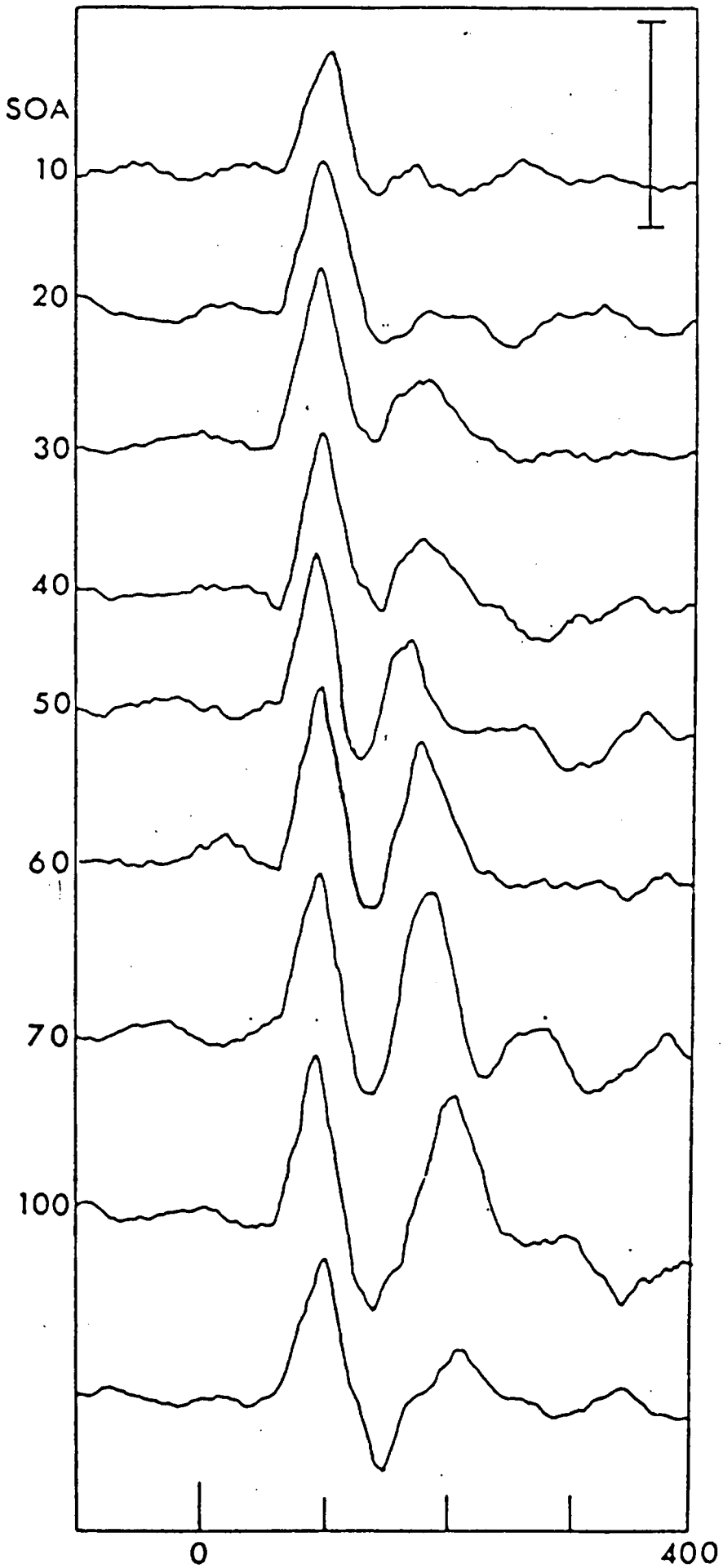


Figure 5.8

VEPs elicited by non-spatially contiguous doublets of 5 msec duration. The lowest VEP was elicited by the first of the doublet pair presented by itself.

that at SOAs of between 40-90 msec the flanking elements of the second stimulus render the first effectively invisible. The precision with which the elements of the doublet contrast pair needs to be aligned suggests that response cancellation reflects some form of retinal interaction.

5.5. General Discussion

In the experiments reported in this chapter response summation and resolution for CI was studied and the resulting summation curves for doublets were found to be the mirror image of those reported in chapter 4 for patterns of the same contrast polarity. The forms of these functions are consistent with those derived from psychophysical studies (reported in the introduction) in that complete negative summation (cancellation) is obtained only at the shortest SOAs (5-10 msec) and only when the stimulus is close to threshold. Where same sign pairs show slight negative summation, doublets produce slight positive summation. Ikeda (1965) has reported a similar interaction at SOAs of 40-80 msec SOA for opposite contrast pairs having equal threshold values.

Comparable psychophysical studies of threshold summation for contrast stimuli have been reported by Watson & Nachmias (1977) and Green (1980) for gratings phase shifted by 180 degrees. It is indeed curious that despite the widely differing experimental conditions and stimulus types (spots or gratings) all studies report that doublets seem to produce a summation curve almost identical in time course. This is all the more surprising given that Rashbass (1970) had used stimuli subtending 30 degrees, whilst Meijer et al (1978) had used spots of less than 11°arc.

Those various models (Roufs,1973; Rashbass,1970; 1976) that have been proposed to account for double pulse summation are not directly applicable to the present data because each has included a threshold detector. However a consistent line of argument has been that the system has a diphasic response, composed of both positive and negative parts and several attempts have been made to describe the time course of these two postulated responses (see for example Roufs,1973; Kelly,1973; Ikeda,1965). A similar conclusion was reached by Grusser & Kapp (1958) from a study of cat retinal ganglion cell activity under double pulse stimulation. Summation, inhibition and duplication of spike activity was reported as the interval between the two same sign

flashes was increased. To account for this, Grusser & Kapp proposed a hypothetical triphasic response function caused by the presentation of a positive flash to the system, prior to the level of spike discharge, that is composed of a large positive, a large negative and finally a small positive part. If such a function were to exist, and to be reversed in the case of a negative flash (ie a brief and spatially restricted decrease in luminance), then the psychophysical data for both same and opposite sign pairs would be readily explained because linear superimposition of these two responses over a range of SOAs will produce a function similar in shape to that obtained experimentally (see Ikeda,1965).

It is however debatable whether such a function is physiologicaly realistic. It is possible, however that the physical basis for the function may lie at the level of the phototransduction process, since the time course of the interaction is similar in both the VEP and psychophysical studies, and the dependence upon exact spatial superimpostion of the opposite contrast elements and the predicted lack of interocular transfer of the effect are all consistent with this notion.

There have been many attempts to model the visual system's temporal response to incremental threshold stimuli (de Lange,1952, see also chapter 4). Two recent models, those of Roufs (1974) and Rashbass (1970; 1976) have had some success. They are not directly applicable to the VEP data in that each contains a threshold detector, located, successive to a stage of linear filtration.

Although the evidence would suggest that the phenomena investigated in this chapter reflect subcortical interactions, it is clear that the output from a specific (striate) region of visual cortex produces a similar function to that observed psychophysically.

One aspect of the present VEP data for which there is apparently no psychophysical correlate is the finding that for doublets the limit of temporal resolution appears to be dependent upon stimulus duration and thus subjective contrast, a curious results which is difficult to explain. The effect would make greater sense if it occurred with decreasing physical as opposed to subjective contrast, as it could be postulated that the effect was a result of the longer integration time constant for low contrast stimuli.

Roufs (1974) has assumed that because threshold summation for incremental and decremental stimuli are the mirror image of those for doublets, the system is essentially linear, with its response to doublets being predictable form its response to incremental and decremental pairs. The present results would suggest that at the electrophysiological level this is not strictly the case. For incremental and decremental pairs it appears that the second stimulus interacts with the response to the first, initially in a cooperative manner and then in an antagonistic fashion. For doublets, however, the second stimulus appears to interact at short intervals in an antagonistic manner than in an cooperative manner, after which the response to the first stimulus affects that of the second, in antagonistic manner; this suggests a non-linear system.

Psychophysical evidence also suggest that the interactions observed with doublets are not predictable from those seen with incremental and decremental pairs. For example, Meijer et al (1978) have shown that for both incremental and decremental stimuli the negative dip in the summation curve at 50-80 msec is stimulus size dependent. Watson & Nachmias (1977) have reported that the effect is also spatial frequency dependent (see figure 5.9). However Meijer et al report that the positive summation observed at SOAs of 50-60 msec for doublets is in fact independent of stmulus size. They suggest that other mechanisms may be active in determining the response to doublets.

It is possible that whatever this mechanism may be, it is responsible for the poorer resolution observed here for CI. Unfortunately this is at the moment pure speculation, no other data have been reported similar to those reported here. One must await physiological studies to explore, under comperable stimulus conditions, the properties of single units located within the retino-cortical pathways in order to determine the exact locus, and type of neural interactions producing this effect.

Chapter 6:- Temporal resolution of flickering stimuli

Introduction

In chapter 4 it was estimated, on the basis of the properties of CI, that the limit of temporal resolution of the retino cortical pathways in man was 40-50 msec SOA, a value that was consistent with both single unit and psychophysical data. It was noted however that this critical value for brief discrete pairs is significantly higher than that which would be predicted on the basis of the CFF.

When scaled in terms of temporal frequency, a limit of temporal resolution of approximately 40-50 msec SOA is equivalent to a CFF of 20-25 Hz. This value, extrapolated from electrophysiological and psychophysical results, is approximately half the CFF measured at comperable adaptation levels and is almost 1.5 times lower than the value obtained by Van der Tweel & Lunel (1965) for high frequency, steady state potentials evoked by luminance modulated fields. Most of those studies which have compared the psychophysical CFF, and that determined on the basis of the VEP, have used luminance modulated stimuli and as noted by Van der Tweel & Lunel (1964) and Regan (1972), have found no clear relationship. Those studies which have used patterned stimuli, report a closer relationship between VEP properties and subjective CFF. For example, Cavonius & Sternheim (1972) report that the extrapolated curve of the steady-state VEP amplitude evoked by counter phase modulated gratings predicts almost exactly the CFF determined psychophysically. Unlike Van der Tweel & Lunel (1964), they did not observe potentials above the subjective CFF of approximately 40 Hz; a difference presumably attributable to the use of pattern as opposed to luminance stimuli.

However, it is not known whether VEPs elicited by the presentation of patterns at high temporal frequencies are generated by the same cortical mechanisms that produce the transient pattern-onset VEPs, although Spekreijse (1977) has suggested that medium frequency VEPs may be produced by the same generator as CII. But since he does not define CII in terms of scalp distribution and pattern specific properties, it is not known whether the negative potential recorded by him is indeed CII. Any negative potential recorded from a midline electrode to lower half field stimulation is not necessarily CII.

In this chapter, experiments were conducted to examine the relationship between the electrophysiologically and psychophysically determined CFF for patterned stimuli. The aim of this study is to compare these values of temporal resolution with those obtained in chapter 4 for brief discrete pairs. The discrepancy between limiting resolution observed for a continuous series and for pairs of brief discrete stimuli will be investigated by examining the VEPs elicited by an intermittent flicker train. Van der Tweel & Lunel (1964), in an extensive investigation of potentials evoked by such stimuli, report that for some subjects at least the output obtained to trains of 500 msec duration, modulated at a frequency of 11 Hz, has properties consistent with that of a resonance filter, the potential amplitude increasing as the period from flicker train onset increased before decaying gradually after stimulus offset. These results clearly question Pieron's assumptions (see introduction chapter 4) about the cause of the poorer resolution of brief discrete pairs; although Van der Tweel & Lunel had used luminance modulated stimuli, it would be unlikely that patterned stimuli would produce such results. The relationship between these types of stimulation will be compared in detail in section 6.4.

In common with most VEP studies, those which have examined potentials evoked by stimuli presented at high temporal frequencies have assumed that the activity recorded reflects some 'generalised' response of the 'visual cortex' (Cavonius & Sternheim,1972). In contradiction to this assumption, I will argue that VEPs elicited by patterned stimuli modulated at high frequencies reflect only the activity of that region of the visual cortex which generates the CI component of the transient pattern-onset VEP. The properties of those components of predicted extrastriate origin, make them unlikely to contribute to VEPs recorded under these conditions. To examine these predictions, the retinal location dependency of high frequency pattern VEPs will be studied. Further experiments will compare the stimulus specificities of the high frequency VEPs with those of CI, and an attempt will be made to link the results to underlying neural mechanisms.

6.1:- Experiment 6.1:- High frequency pattern VEPs Procedure and methods

The stimulus was the same as in chapter 4, i.e., a regular dot pattern whose elements were of positive contrast with reference to the background field. Background luminance was set at 400 cdm^{-2} and the contrast of the elements set to 0.20. Stimuli were presented in tachistoscope A. Temporal frequency was determined by a function generator, its output fed into bistables, which in turn triggered the stimulus fields. The onset of the cycle switching the stimulus field also triggered a Digitimer which was set to a cycle period of 600 msec. This in turn triggered the computer which sampled for 500 msec. Seven runs of 15 sweeps were undertaken for each condition.

Electrode positions

The electrode locations used in this experiment were the standard bipolar placements used to record CI, because it is assumed that high frequency pattern-onset VEPs are generated in same cortical area as CI. In experiment 6.2 this assumption will be examined in greater detail.

Results

In figure 6.1 are shown the waveforms obtained to either left half-field or lower left quadrant-field stimulation. Previous surface mappings had shown that for this subject, under these conditions, the stimulation of the lower quadrant is most effective for eliciting CI. The major positive potential in the waveform obtained at 1 Hz is therefore CI which under these conditions has a peak latency of 90-92 msec.

Evident in the waveforms obtained for left half-field stimulation for frequencies of between 5-15 Hz, is a second response other than that of the fundamental. By 15 Hz this second peak has disappeared. This activity is clearly related to the offset of the pattern, as is shown by the dashed waveforms in column B of figure 6.1, where instead of triggering the computer from stimulus onset, averaging commenced from stimulus offset which elicites a VEP that is 180 degrees out of phase with regard to that produced when triggered from stimulus onset. The important waveform is that recorded at 1 Hz, for there it can been seen that the offset of the pattern at low temporal frequencies produces a characteristically double peaked OFF response. As the frequency of stimulation is increased the off response will move toward the on response. Since the off response (which for the transient

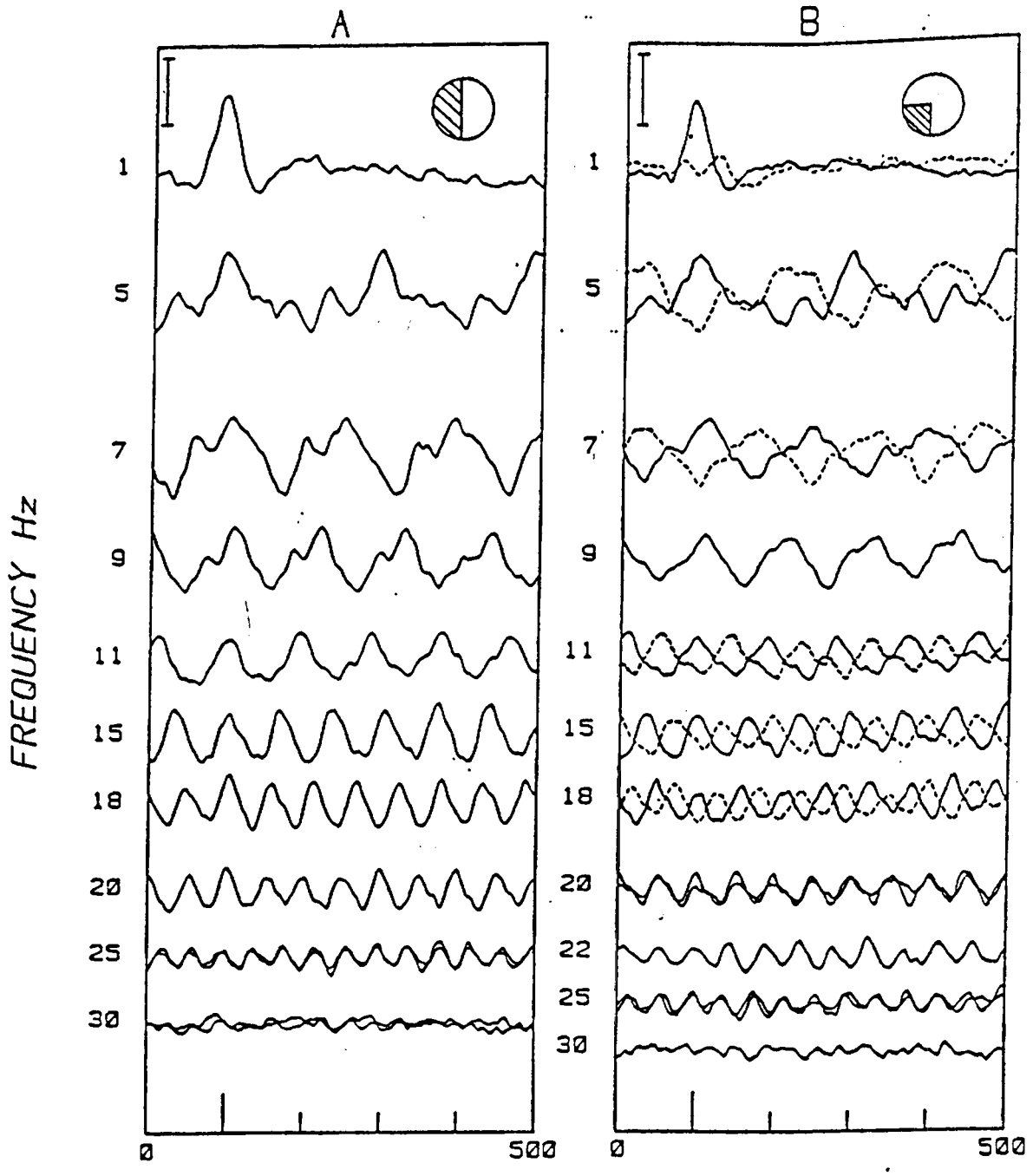


Figure 6.1

VEPs recorded to left (column A) and lower left quadrant (column B) stimulation with regular dot patterns modulated at frequencies indicated at the side of each column. The dashed waveforms in column B were recorded when the computer was trigger at stimulus offset, which at 1 Hz shows the doubled peak 'off' response. Each waveform is the sum of 7 runs of 8 sweeps, as are all subsequent waveforms shown in this chapter.

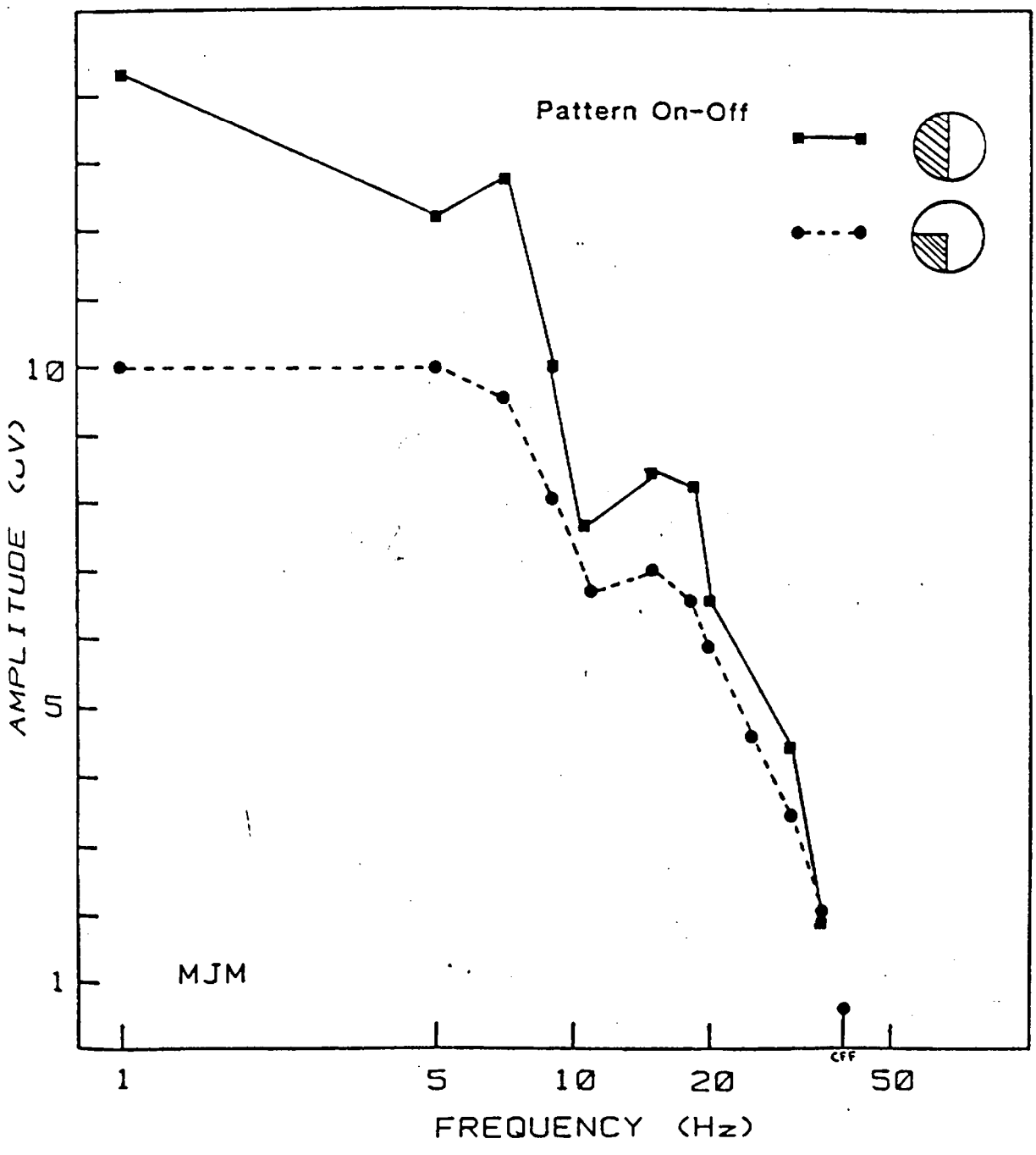


Figure 6.2

Plots of mean peak-to-peak VEP amplitude as a function of temporal frequency, for left and lower left quadrant stimulation. The psychophysically determined CFF is indicated by the 'up' arrow on the abcissa. Data for one subject.

stimulation can be shown to have a different scalp distribution and therefore a different source locus from that of the on-response) disappears at a temporal frequency of 15 Hz this is consistent with the durations lower than 60 msec under transient stimulation; which is equivalent to a stimulus modulated at a frequency of approximately 15 Hz. (The implications of this conclusion will be discussed in greater detail in the discussion section below).

The main finding of this experiment is that VEPs can be evoked at temporal frequecies of up to approximately 35 Hz, and that the slope of the amplitude Vs modulation frequency curve, when extrapolated to the baseline, predicts closely the psychophysically determined CFF, for both the left half-field and lower left quadrant-field response, figure 6.2. Peak amplitude has here been determined by taking the mean peak-to-peak voltage for the 500 msec sample. Thus the limit of temporal resolution is higher for steady state conditions than for VEPs evoked by brief discrete pairs, a finding which is consistent with the available psychophysical data (see for example Boynton,1973).

6.2:- Scalp Distribution of high frequency pattern VEPs

It can be shown that for this subject the CI component originates predominatly from stimulation of the left half-field although the relative amplitude of the potential will vary as a function of the position of the pattern within this half field. The following experiments attempt to determine whether high frequency VEPs have a similar dependence on pattern location as CI.

Results

The VEPs to left-half field and lower left quadrant stimulation have been shown in figure 6.2, and in figure 6.4 are shown the VEPs elicited by right half-field and upper right and lower right quadrant field stimulation. It is evident that there is little activity in either half or quadrant field responses at frequencies above 5 Hz. Indeed even at the lowest temporal frequency the response is of smaller amplitude and longer latency than that obtained with left half field stimulation. The VEP at 1 Hz does not appear to contain a significant CI component since the latency of the peak is some 20-30 msec longer than that of CI for the left field and is probably therefore CII (although there may be

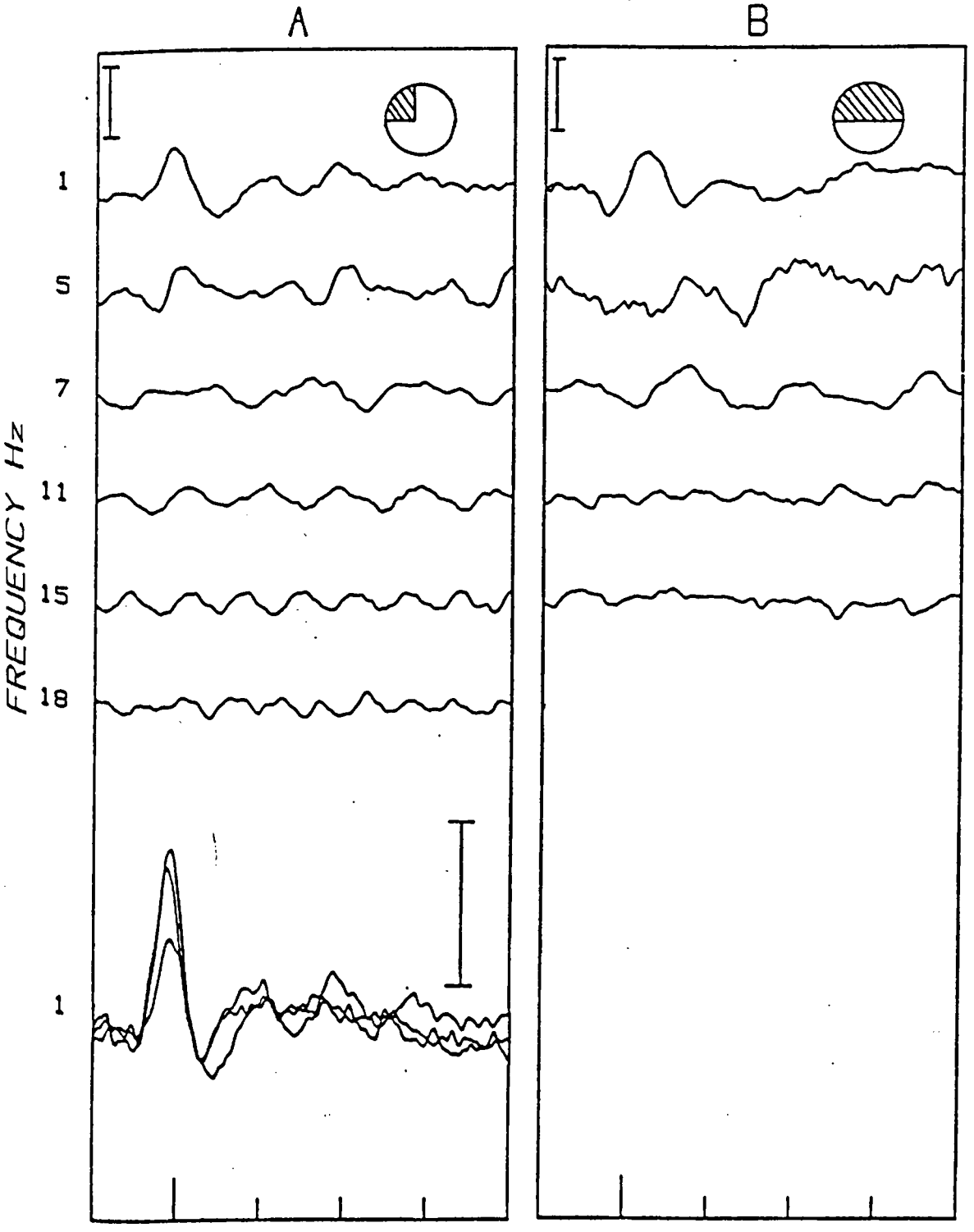


Figure 6.3

Shows the retinal locus (pattern position) dependence of the amplitude of high frequency VEPs.

In column A the waveforms were obtained by stimulating the upper left quadrant, which in this subject under these electrode placement is known to produce CI.

It is known that in this subject the amplitude of CI elicited by transient pattern stimulation will be greater for the lower left quadrant than for the upper. This is illustrated by the VEPs recorded at 1 Hz shown at the bottom of column A. The smaller VEP in this case is from the upper left quadrant the larger two from the left field and lower left quadrant. All are presented at increased gain.

In column B are illustrated the VEPs obtained with upper field stimulation, recorded from a midline electrode 4 cm above the inion with reference to the right ear.

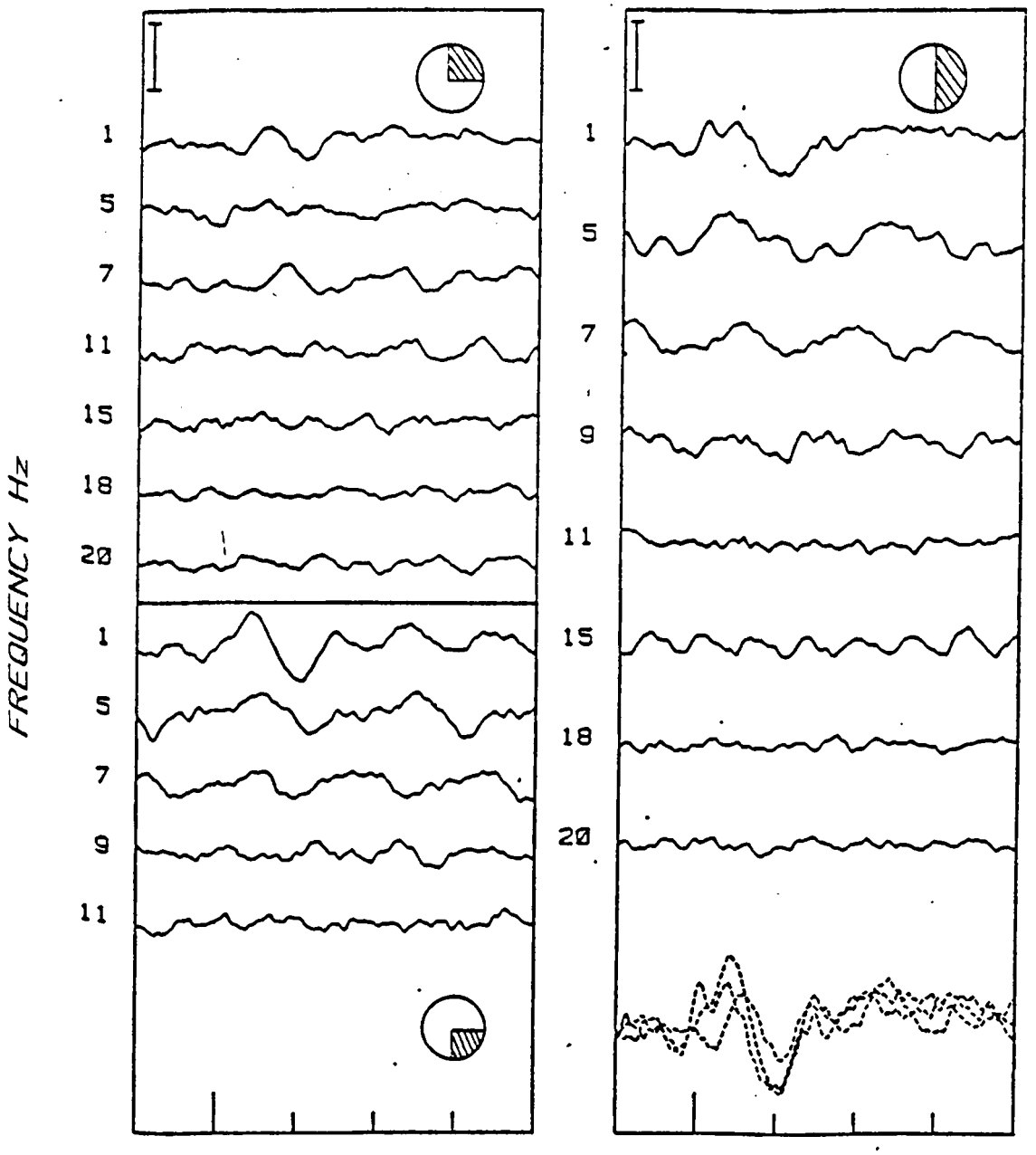


Figure 6.4

The effect of varying the retinal location of the pattern of on the VEP elicited at the bipolar electrode site.

Shown in the right hand column are the VEP recorded from right field stimulation. Those VEPs recorded at the 1 Hz rate are shown at the bottom of this column.

some contribution from luminance related activity). However above 5-7 Hz there is no evoked activity.

In order to determine whether CII is evoked at these medium rates of temporal stimulation the pattern was now confined to the upper half field and a recording was made from a midline electrode 4 cm above the inion with reference to the right ear, the optimal conditions for recording CII in this subject. The waveforms obtained under these conditions are shown in figure 6.3 (CII is positive under these conditions) and it is clear that above 5 Hz there is no stimulus related activity which suggests that the CII component doesnot contribute to high frequency pattern onset stimulation.

6.3:- High frequency pattern, luminance on-off and pattern-reversal VEPs

The above data suggests that high frequency pattern VEPs have a similar retinal locus dependency to CI, and that therefore they originate from the same region of the visual cortex. In this section the properties of these VEP are compared in detail with those of luminance onset and pattern-reversal.

There have been reports (e.g. Spekreijse et al,1977) that for sinusoidaul luminance modulation, frequency doubling can be observed at repetition rates of 3-11 Hz. This phenomenon has also been reported to pattern-onset stimulation where the response doubling is found up to frequencies of 12-15 Hz.. As was shown in section 6.1, this effect can be attributed to the occurrence of 'off' responses. It is not known whether this is also the cause of the frequency doubling observed with luminance modulated fields.

A second reason for conducting these experiments was to compare the waveforms obtained to pattern-onset with those obtained to pattern-reversal. Finally a comparison between the phase and retinal field dependency of these forms of high frequency VEPs will provide a check as to the pattern specifity of the potentials reported in experiment 6.1.

Methods and procedure

The conditions and mode of experimentation were similar to that reported above with the exception that in the present case checkerboard stimuli were used because their equal mark space ratio allows

pattern-reversal stimulation. Contrast was again set at 0.20. Monopolar responses were recorded with reference to the right ear.

Psychophysics

In order to determine any possible relationship between the properties of these high frequency VEPs and subjective CFFs for both pattern and luminance modulation, a short psychophysical experiment was undertaken. Subjective CFF was determined by a staircase method of limits technique (Kling & Riggs,1972). Starting at a frequency which could easily be discriminated as flickering, stimulus frequency was increased in steps of initially of 5 and then 2 Hz until the subject no longer reported being able to detect temporal modulation. This point was then recorded and the procedure repeated, this time decreasing stimulus frequency from some high value down to the point at which the subject reported flicker. Ten trials, five up and five down the scale were undertaken and the mean of the ten values taken to be the CFF for each of the three subjects all of whom were experienced observers.

Results

The results of this experiment are shown as bar histograms in figure 6.5a. CFF for all subjects and both conditions are very similar although CFF for luminance modulation is some 2-3 Hz higher than pattern CFF in all three subjects; similar values have been reported by Cavonius & Steinheim (1972) and Kelly (1970). It will be shown below that the psychophysically determined CFF is similar to that obtained by extrapolating the slope of the VEP amplitude modulation frequency to the baseline. Thus both types of data are in agreement in showing that the limit of temporal resolution for steady state conditions is some 12 Hz higher than would be predicted the basis of the limit of temporal resolution for similar stimuli presented as brief discrete pairs.

VEP Results

The waveform shown in figure 6.5b were obtained from lower left quadrant presentation both pattern on-off (A) and reversal (B) stimuli. The comparable waveforms for luminance modulation are shown in figure 6.6 (A) along with waveforms obtained by stimulating the upper right quadrant. At the 1 Hz stimulation rate CI is readily identifiable with pattern on-off, the pattern-reversal response at the same repetition rate is more complex in that a broad double peak is evident. It is

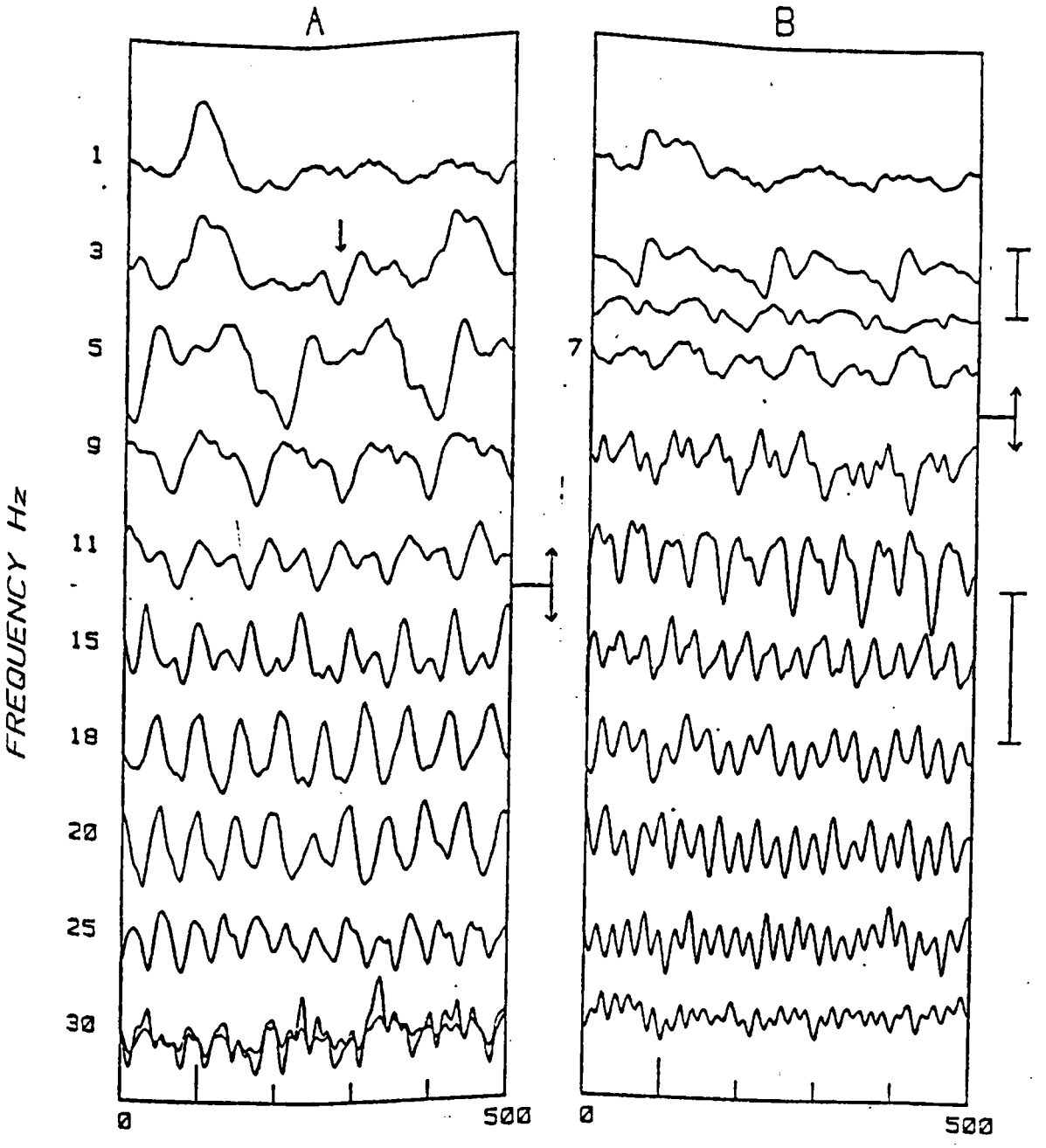


Figure 6.5b

VEPs elicited by pattern-onset (column A) and pattern reversal (column B). For waveforms above the arrows the gain has been reduced (see 10 uv calibration bar), those below the line are twice gain. VEP were recorded to stimulation of the lower left quadrant of a 9 degree field. At 30Hz in column A the waveform has been further increased in gain by a factor of two. See text for discussion.

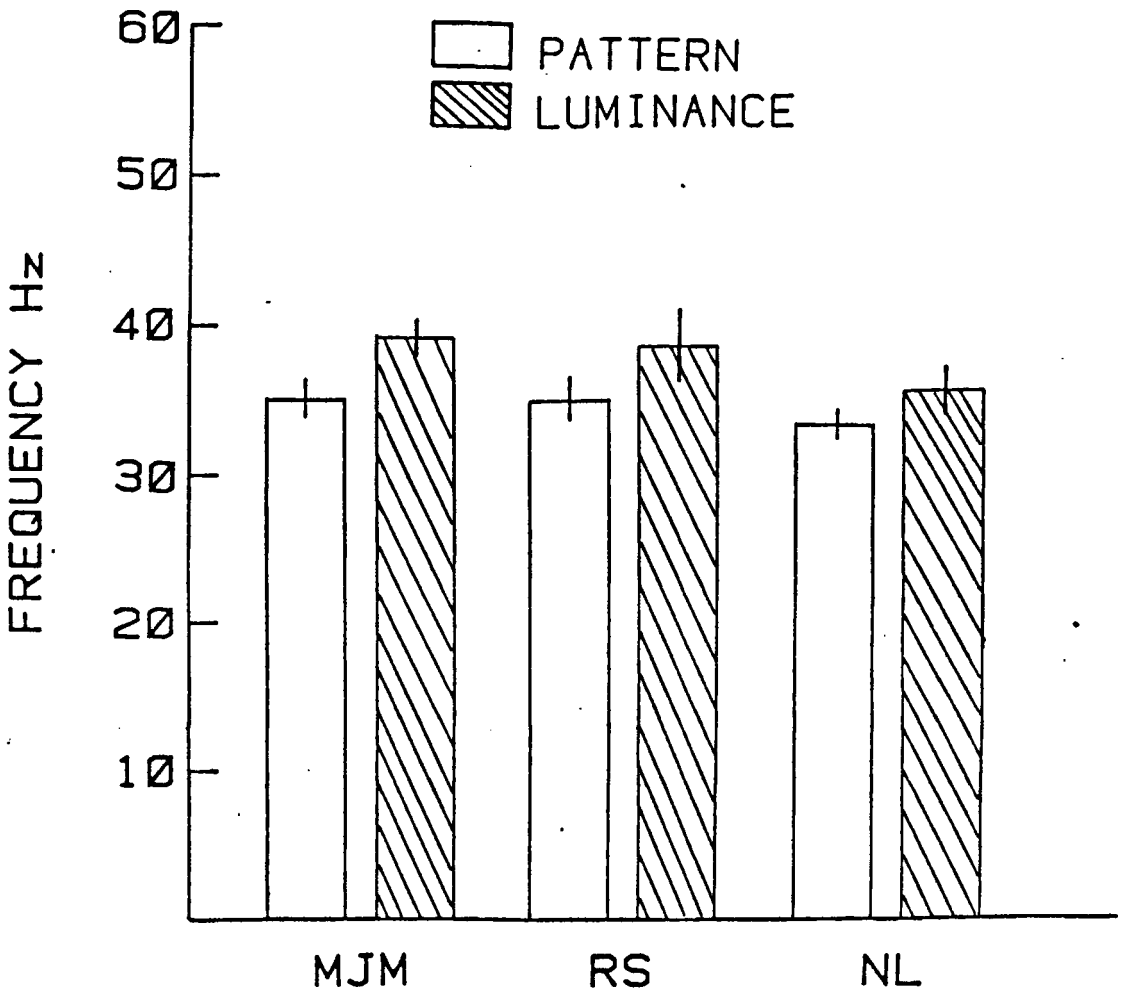


Figure 6.5a

Psychophysical CFF plotted as bar histograms for the three subjects studied. The error bars are shown, where significant, and are +- 1 SEM. CFF for luminance modulation is under these conditions higher than that for pattern stimulation. See text for details.

suggested that these peaks reflect the response of both 'on' and 'off' mechanisms. The small amplitude of the onset response is to be expected since there is likely be to pronounced adaptation of the pattern on response mechanisms under this mode of stimulation.

With increasing temporal frequency VEPs to pattern on-off show evidence of frequency doubling for the range between 3-15 Hz consistent with the results reported in section 6.1. and supporting the conclusion that this 'second harmonic' response is in fact caused by offset activity. The arrow above the 3 Hz waveform indicates the double peaked offset response characteristic of this subject. Again, at frequencies above 15 Hz the waveform appears as a sine wave and only the fundamental response is evident. Responses can be obtained up to repetition rates of 30-35 Hz, which is consistent with the results of the previous section.

Pattern-reversal stimulation produces a different effect, evident at the medium frequency range where for a 9 Hz input a 36 Hz output is obtained. This result can be explained if pattern reversal is producing both 'on' and 'off' responses. At frequencies above 15 Hz the waveform shows a frequency doubled response similar to that reported by Cavonius & Sternheim (1972), which suggests that the system is responding to every change in effective retinal contrast but that activity evoked by stimulus offset has ceased; this would be consistent with the value obtained with the simple 'on-off' presentation mode.

The potentials evoked by the luminance modulation of the whole of the lower left quadrant differ in several ways from both the above forms of stimulation and thus prove that VEPs elicited by patterned stimuli cannot be explained in terms of luminance changes. Firstly, at low temporal frequencies the onset of a luminance step does not evoke a specific potential, at least when recording between these bipolar electrodes. Although when recording between monpolar electrodes with reference to the right ear a potential can be recorded at both electrodes (see figure 6.7, where in column C the two superimposed waveforms are recorded at 1Hz from the monopolar, contra- and ipsilateral electodes). This VEP is positive in each case and longer in latency than of the pattern-onset VEP recorded at the contralateral

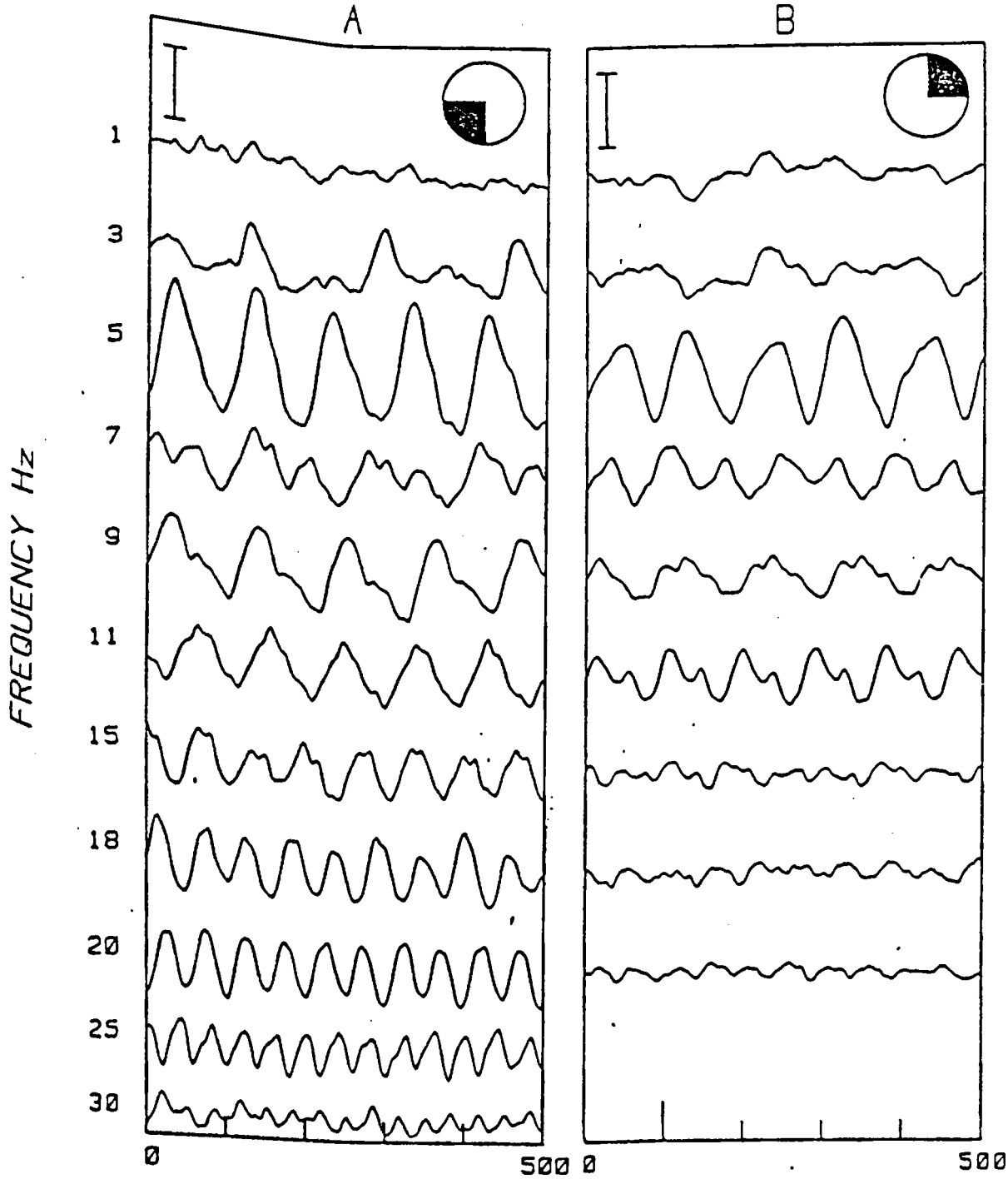


Figure 6.6

VEPs elicited by luminance modulation. VEPs shown in column A can be compared to those shown in figure 6.5b, notice the absence of activity at 1 Hz and the marked increase in amplitude up to 5 Hz.

In column B waveforms obtained under the same conditions as above but with upper right quadrant stimulation. Compare these with those illustrated in column A of figure 6.4.

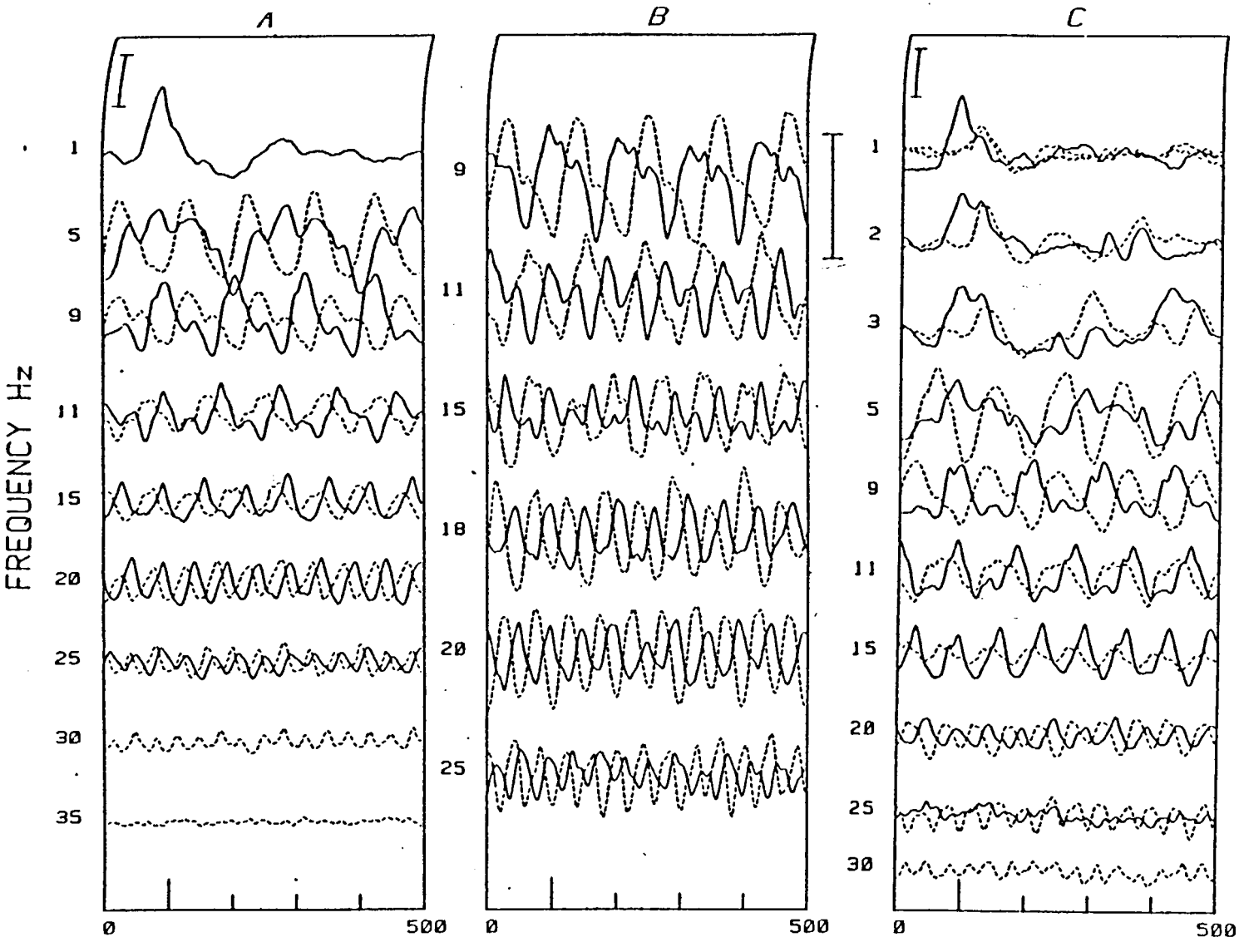
Figure 6.7

VEPs recorded to pattern (continuous trace) and luminance (dotted trace) modulated stimulated.

In column A are illustrated bipolarly recorded waveforms for stimulation of the left quadrant.

In column B are illustrated waveforms obtained in a second experiment. The waveforms shown in column B are however increased in gain by a factor of 2. Luminance VEPs and pattern VEPs are approximately 180 degrees out of phase up to the limit of resolution.

In column C are shown the simultaneously recorded monopolar (contralateral electrode, ref right ear) electrode VEPs. The luminance VEPs at 1 Hz (dashed trace) are recorded from both the monopolar (contra and ipsilateral) electrodes.


A
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C
FREQUENCY Hz
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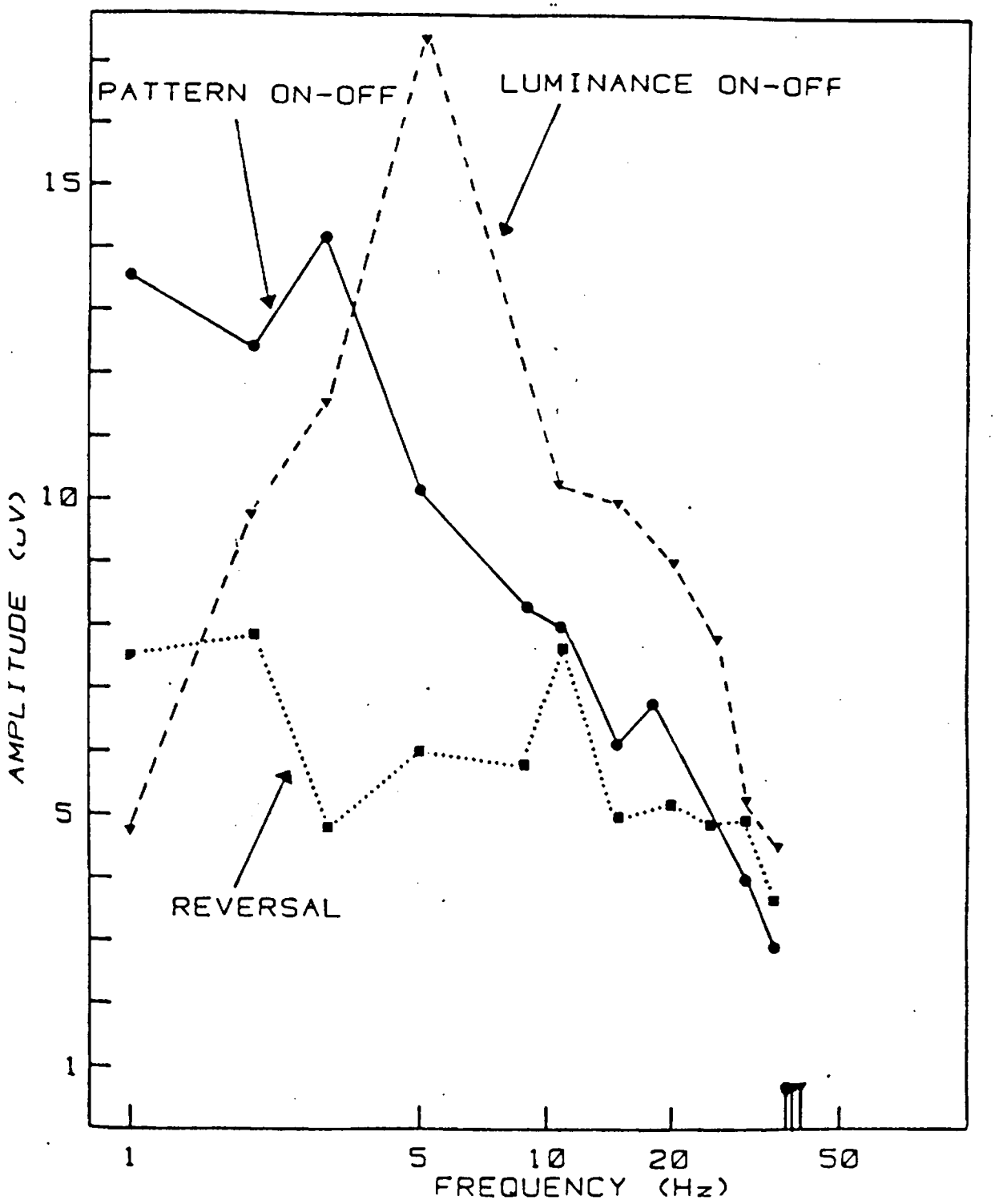


Figure 6.8

Plots of peak-to-peak amplitude as a function of temporal frequency for the three types of stimulus conditions used. The psychophysically determined CFF are indicated on the abcissa by the appropriate symbols.

electrode. The latter mode of stimulation produces little if any evoked activity at the ipsilateral electrode. The polarity of luminance VEPs does not reverse across the midline and is independent of stimulus location and electrode position.

The second major difference is that frequency doubling is evident in the VEPs between 3-9 Hz, with the potentials evoked at 5 Hz becoming as large as 20 μV. Frequency doubling is absent at 11 Hz, which is 4 Hz lower the was observed for patterned stimulation. It is at the high frequency end of the scale that luminance VEPs become more consistent and pronounced, and they can be evoked up to repetition rates of 30-35 Hz.

In figure 6.8 potential amplitude has been plotted as a function of temporal frequency and, as was evident in the waveforms themselves there are major differences between the three modes of presentation. For both luminance and pattern reversal stimulation there is clear low frequency attenuation. With pattern reversal the slope of the curve appears flat across most of the low to medium frequency range, dropping off, at a shallow rate, only at the highest frequencies.

Luminance modulation produces a sharply tuned response, peaking at approxiamately 5 Hz with pronounced low frequency attenuation and a sharper high frequency fall off; the slope of the curve clearly extrapolating to the psychophysically determined CFF. The low frequency attenuation observed for luminance VEPs is similar to that obtained in psychophysical measurements of temporal modulation transfer function (TMTF), although it should be noted that the comparable VEP attenuation observed with pattern-reversal stimulation apparently has no psychophysical counterpart (see Kelly,1970), and was not reported by Cavonious & Sternheim (1972). This suggests that the VEPs recorded by these workers reflect some different type of cortical activity. [It is evident that CFF for the luminance modulation recorded here is some 30-40 Hz lower than the value reported by Van der Tweel & Lunel (1964) and by Regan (1970). Direct comparisons across studies are difficult, because electrode positions vary in each case. However I was never able to record activity above subjective CFF. Whether this fact reflects some underlying difference as to the generators of these luminance potentials with regard to those recorded by the above authors is not known. It should be noted however that in both of the above studies large, 30 degree and 60 degree fields were used as opposed to the 4.5 degree half-field or quadrant used in this study. This substantial

difference in field size may therefore be the crucial factor].

Pattern onset stimulation does not produce low frequency attenuation, and as would indeed be expected, the slope of the curve is similar to that obtained in section 6.1 for regular dot patterns.

The third major difference between these modes of presentation is evident in figure 6.6 where the responses obtained to the stimulation of the upper right quadrant with a luminance modulated stimulus have been shown. These waveforms show that luminance VEPs are independent of retinal locus, the peaks of the waveforms record by stimulating the upper right quadrant are in-phase with those of the lower left quadrant, consistent with the suggestion that they originate from non-retinotopically organised regions of cortex.

The final evidence to show that high frequency pattern and luminance VEPs reflect different activity is presented in figure 6.7. The waveforms in column A and B were obtained in two different experiments under the same conditions and show that luminance and pattern VEPs are approximately 180 degrees out of phase with respect to each other, this effect occuring up to the limit of subjective CFF. This phase difference is, furthermore, independent of electrode derivation as is indicated in column C, where the monopolar responses recorded from the contralateral electrode have been shown. The implications of these results will be considered in greater detail in the discussion.

6.4:- VEPs to intermittent pattern and luminance flicker trains

Thus far these experiments have shown that the electrophysiological limits of temporal resolution under steady state conditions are higher than those obtained to discrete pairs of brief stimuli. The experiments reported in this section examine the properties of VEPs evoked by flickering trains of pattern or luminance modulation of 500 msec duration.

Methods

Field size and electrode positions were as above. In the present case the lower left quadrant was used, because stimulation of this region of the field effectively isolates the CI component. The contrast

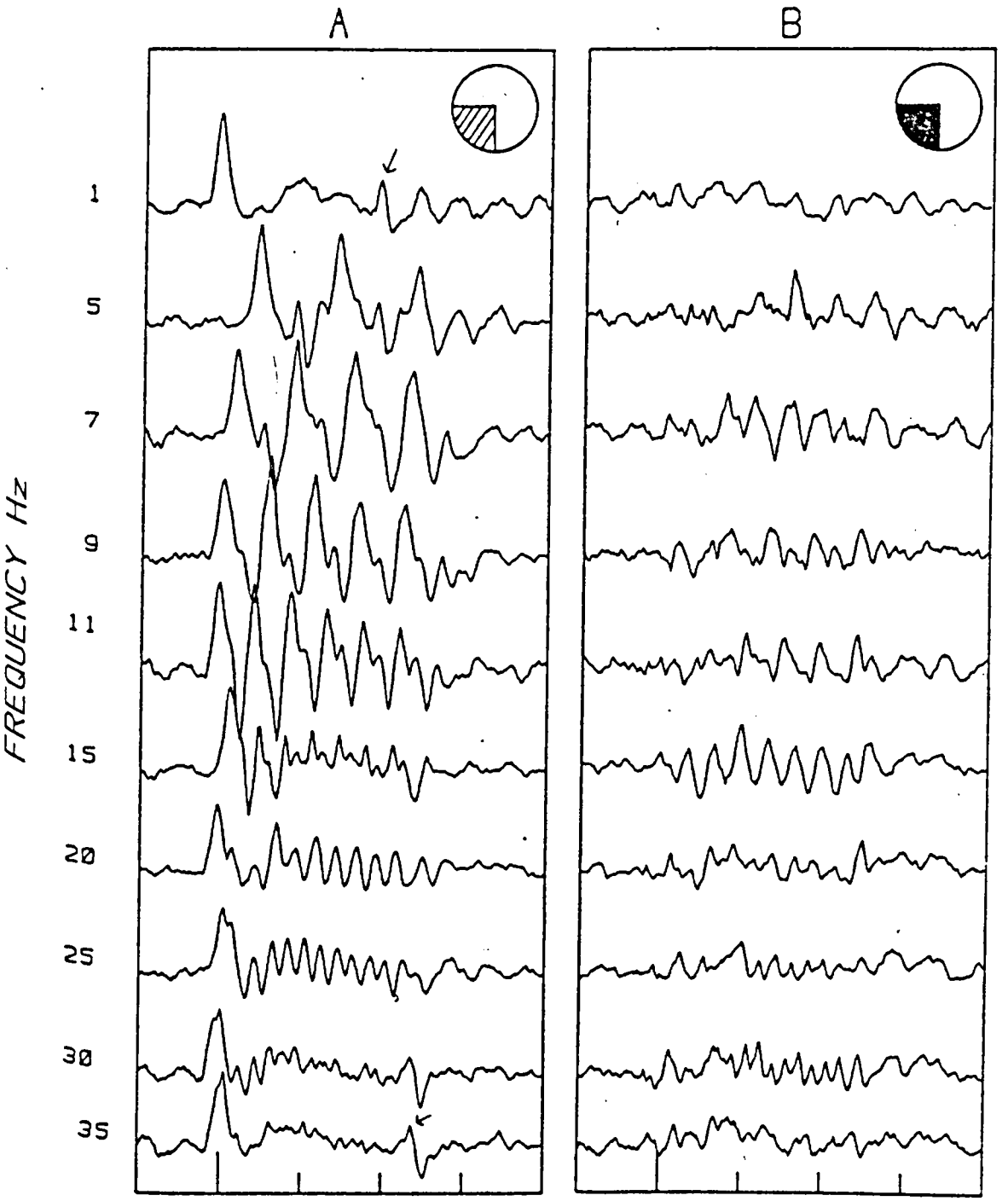


Figure 6.9a

VEPs elicited by pattern (column A) and luminance modulated (column B) flicker trains. Scale is 1000 msec.

of the checkerboard was set at 0.20 and background luminance set to 200 cdm $^{-2}$. Luminance stimulation was achieved by removing the patterned stimulus.

A flicker train of 500 msec was generated by gating the output of a function generator. Because the phase of the function generator was not locked to the start of the Digitimer cycle which triggered the computer averager, the onset of the stimulus train was not fixed in relation to the start of the averaging cycle, which in turn lasted 500 msec. However this was not considered to be too important as the amplitude and form of the response was the variable of interest.

Results and Discusion

Column A of figure 6.9(a) shows the VEPs elicited by the patterned flicker train whilst column B shows the VEPs elicited by the luminance flicker train. In figure 6.9(b) the VEP to the patterned train are presented on a larger scale for clearer representation. In figure 6.9(c) these are superimposed on the response to the luminance modulated train. Several features are evident.

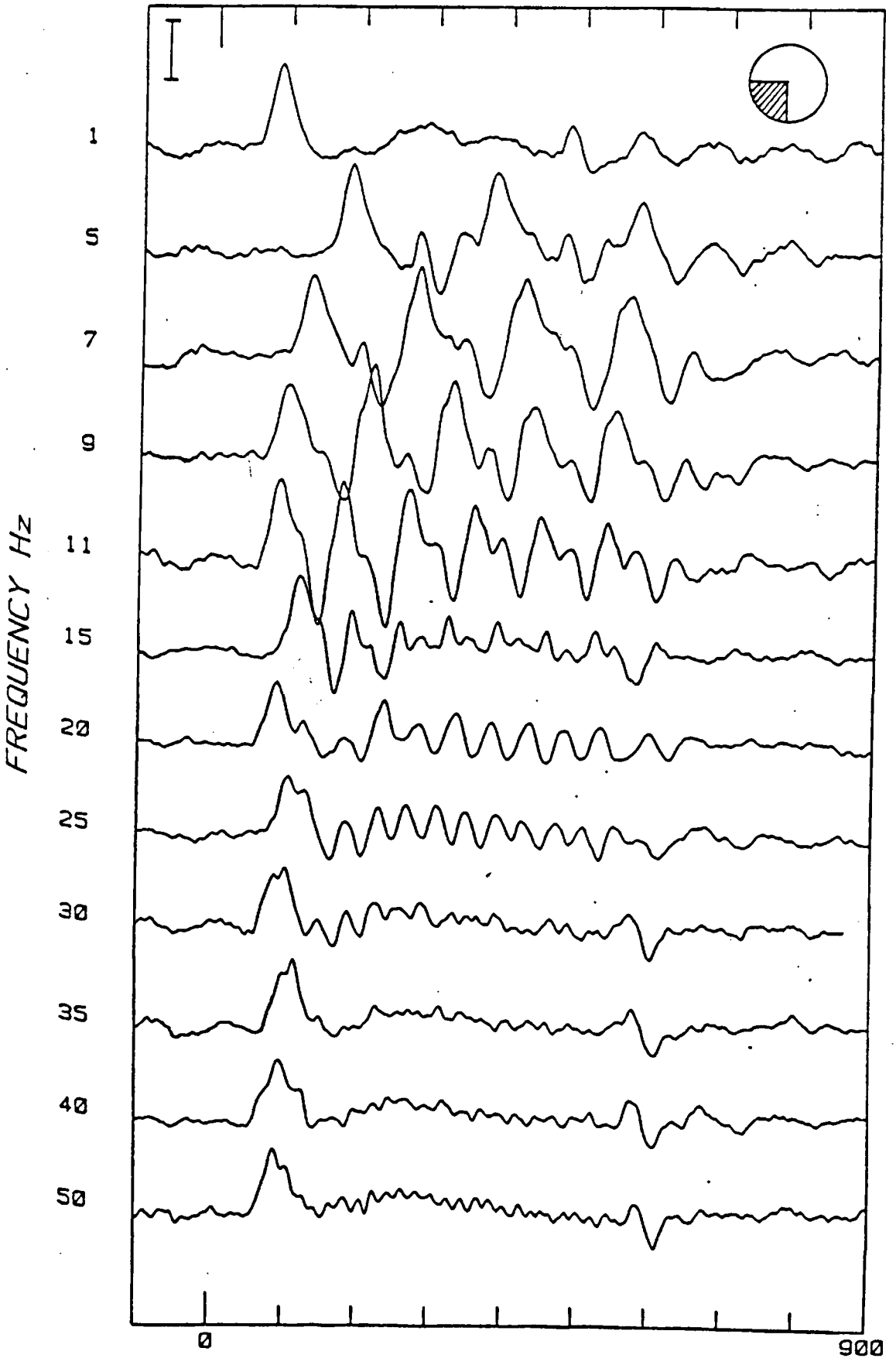
Firstly, for patterned stimulation the first stimulus of the flicker train produces a response which is 'unique' in the sense that it's amplitude is independent of the frequency of stimulus presentation within the train.

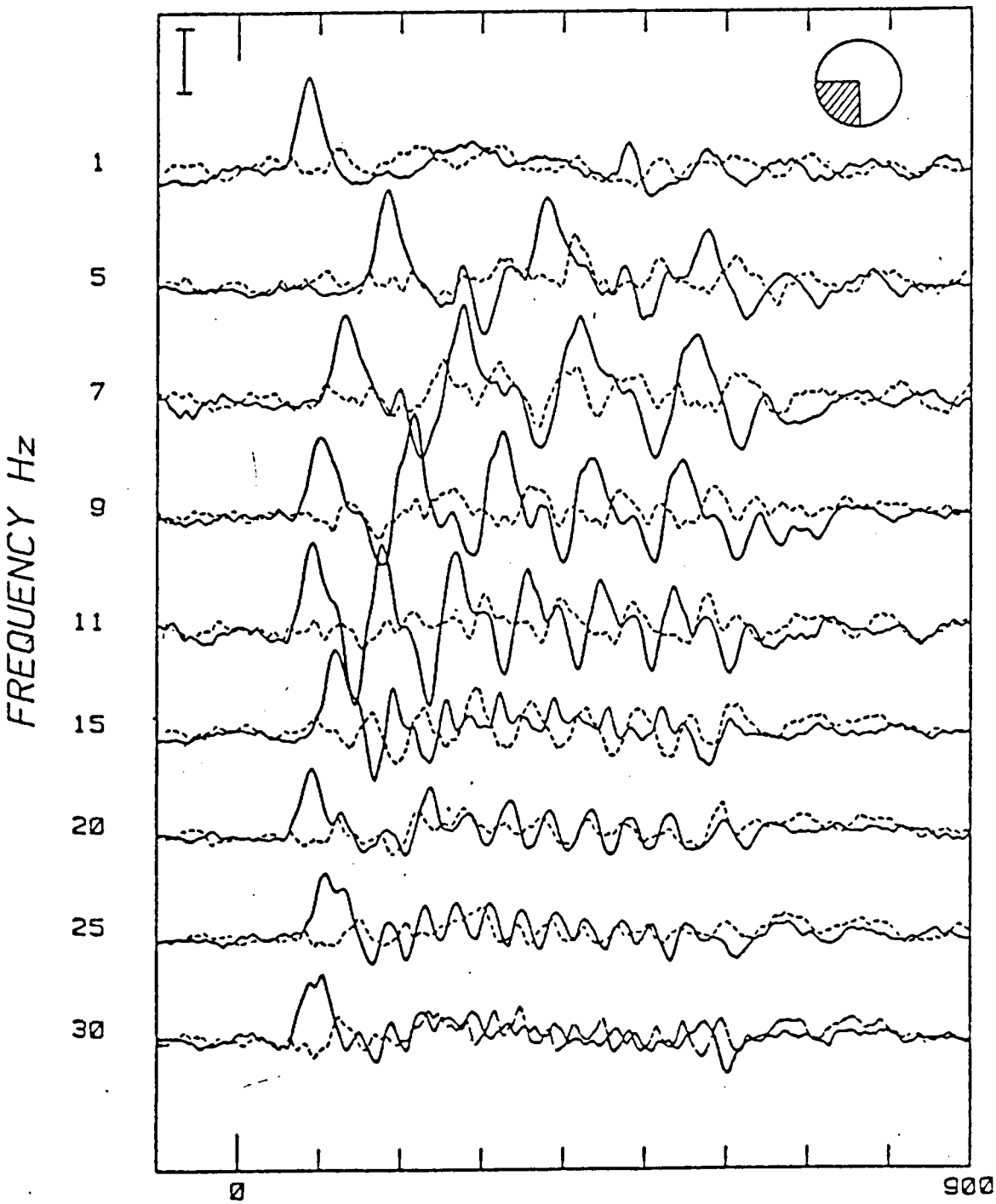
Secondly, at low temporal frequencies, ie below 9 Hz, there appears to be frequency doubling as was observed in experiment 6.1. It can be shown however that, consistent with the potential observed at a latency of 580 msec (arrowed for clarity in the 1 Hz stimulus, i.e., 500 msec duration pattern) this doubling effect is produced by the occurrence of off responses. Thus the waveforms follow the frequency of stimulation up to approximately 25 Hz, which is equivalent to an onset interval of some 40 msec. At higher frequencies the waveform is dominated by the response to the onset of the flicker train such that the VEP, at 35 Hz, appears similar in form to that obtained at 1 Hz. Under these conditions subjective CFF is some 30 Hz, in good agreement with the VEP data.

The VEPs elicited by luminance modulated trains are however curious in that relatively little stimulus related activity is evident (see figure 6.9c). Indeed it is not until the repetition rate has

Figure 6.9b

Illustrating, on a larger scale, the VEPs elicited by pattern flicker trains. Notice that in all cases the onset off the flicker train elicites a large postive VEP which at this electrode location and field of retinal stimulation is for this subject CI. Notice also the consistent 'off' response at higher temporal frequencies.





VEPs to pattern and luminance modulation trains superimposed for a range of temporal frequencies.

Figure 6.9c.

reached frequencies of 7 Hz and above that temporally tuned activity can be recorded. The clearest case of this is seen for the 15 Hz stimulus. It appears that with luminance modulation, unlike pattern modulation, the system behaves as a frequency resonator; the amplitude of the response increasing as the time interval from the onset of the flicker train increases.

6.5:- High frequency contour and contrast VEPs

In chapter 7 it will be shown that the latency of CI is dependent on the spatial frequency or element width of the stimulus pattern, increasing with decreasing stimulus size. Thus when stimuli containing isolated squares of a range of square sizes from 1 degree to 6' arc, are presented the latency of response increases progressively over the range by approximately 20-25 msec. However when these same squares are presented not as full contrast squares, but as outline squares, where the width of the line is some 0.6' arc, it is found that the latency of CI is in fact independent of square size, even for squares up to 1 degree in side length. It is assumed that the outline stimuli preferentially activate those mechanisms processing high spatial frequencies and that this activity will be 'closely related' to those mechanisms producing the contour specific activity of CI, (see Jeffreys, 1977).

Thus if the high frequency pattern VEPs do indeed originate from the same cortical region as CI, then such VEPs obtained to full contrast squares and outline squares should have similar properties to that observed for CI. That is the latency of response, phase, of the high frequency waveform should differ in the two conditions. Moreover the difference should be independent of the rate of temporal modulation although the amplitude of steady state responses to the outline stimuli should show a more rapid high frequency cut off, consistent with the fact the subjective CFF for this stimulus will be lower. In the following experiment I have attempted to investigate these predictions.

Methods

Stimuli were presented to the left half field. Contrast was 0.20. and square size ranged from 9' arc to 54' arc. The outline squares were similar in size and spacing but were defined only by a thin (0.6' arc) line. One subject was used, and six runs of 10 sweeps were undertaken

at a range of stimulus frequencies. Stimulus contrast and background luminance was as above.

Results

The VEPs produced by these isolated square patterns have been shown in figure 6.10(a-d). The response to all four contrast squares have been superimposed to give some indication of the form of the response and its consistency, as is shown in figure 6.10(e).

A number are features are evident. Firstly, at the lowest temporal frequency, (1 Hz), the major peak is that of the CI component which for each stimulus is of a shorter latency with full contrast squares than with outline squares (see figure 6.11 for values, determined at the 1Hz stimulation frequency).

Secondly, the off responses observed at 3 Hz (arrowed for clarity in each figure), larger for contrast squares than for outline squares. This is a consistent feature of the off-response complex and is observed under transient pattern-onset stimulation (see Chapter 13). Thirdly, the latency differences between full contrast squares and outline squares increases with increasing overall square size and this occurs up to the limit of temporal resolution for the outline stimuli. Thus comparing the 15 Hz waveforms evoked by all square sizes it is evident that the response evoked by contrast and outline squares of 54'arc are 180 degree out of phase, which at this temporal frequency is equivalent to a latency difference of approximately 33.3 msec, this value is similar to the actual latency difference observed at 1 Hz for full contrast and outline squares of this size.

It is evident however, that the response to large 54'arc and 42' arc, full contrast squares contain two peaks; the second longer latency peak has a value similar to that for outline squares of similar size. This effect is also observed with transient pattern stimulation with squares of this dimension, and support the notion that the CI component evoked by contrast squares contains two types of activity, one contour and the other, contrast specific. Thus with full contrast squares of large dimension the contrast specific response, (which has a reduced latency with increasing element size), will be some 20 msec earlier than than the activity of the contour processing mechanism which is presumably responding to the edges of the squares. Thus, as is evident at temporal frequencies of 1-7 Hz for both 42-54'arc. squares this

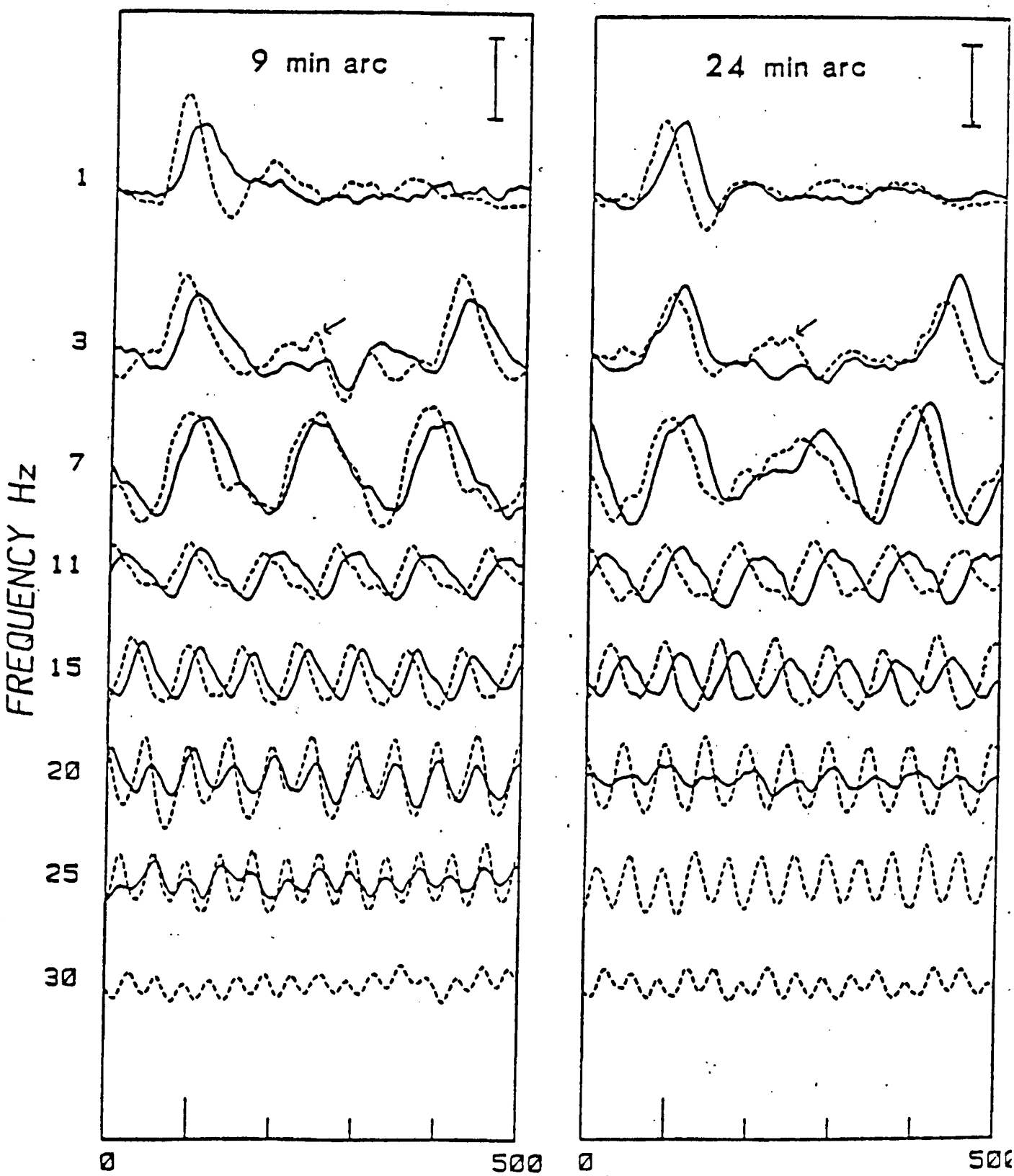
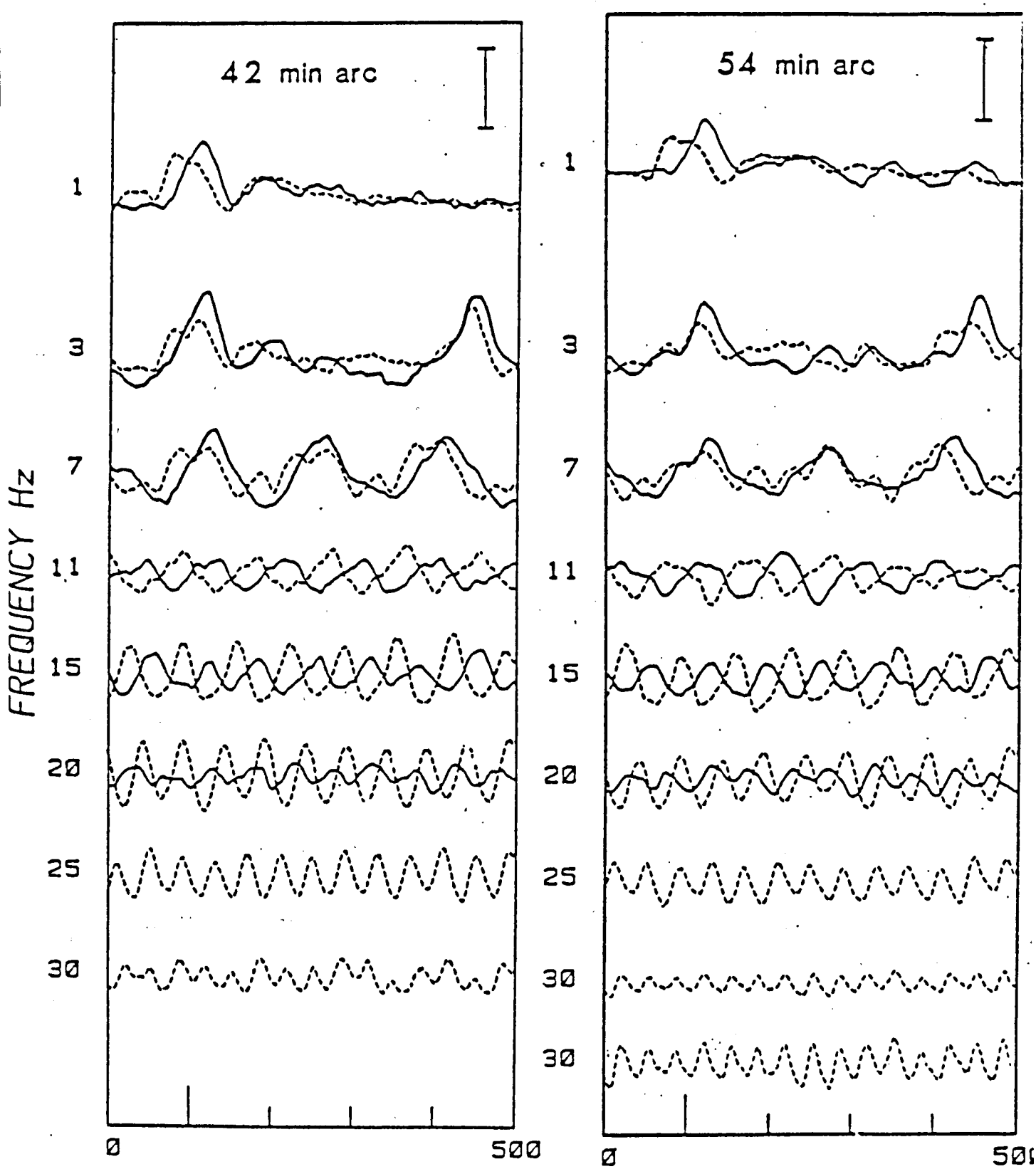


Figure 6.10a-b

VEPs obtained to contrast and outline squares of varying square size. Those elicited by contrast squares are shown in the dashed trace, those in the continuous trace are for outline squares.


42 min arc
54 min arc
FREQUENCY Hz
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20
25
30
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500

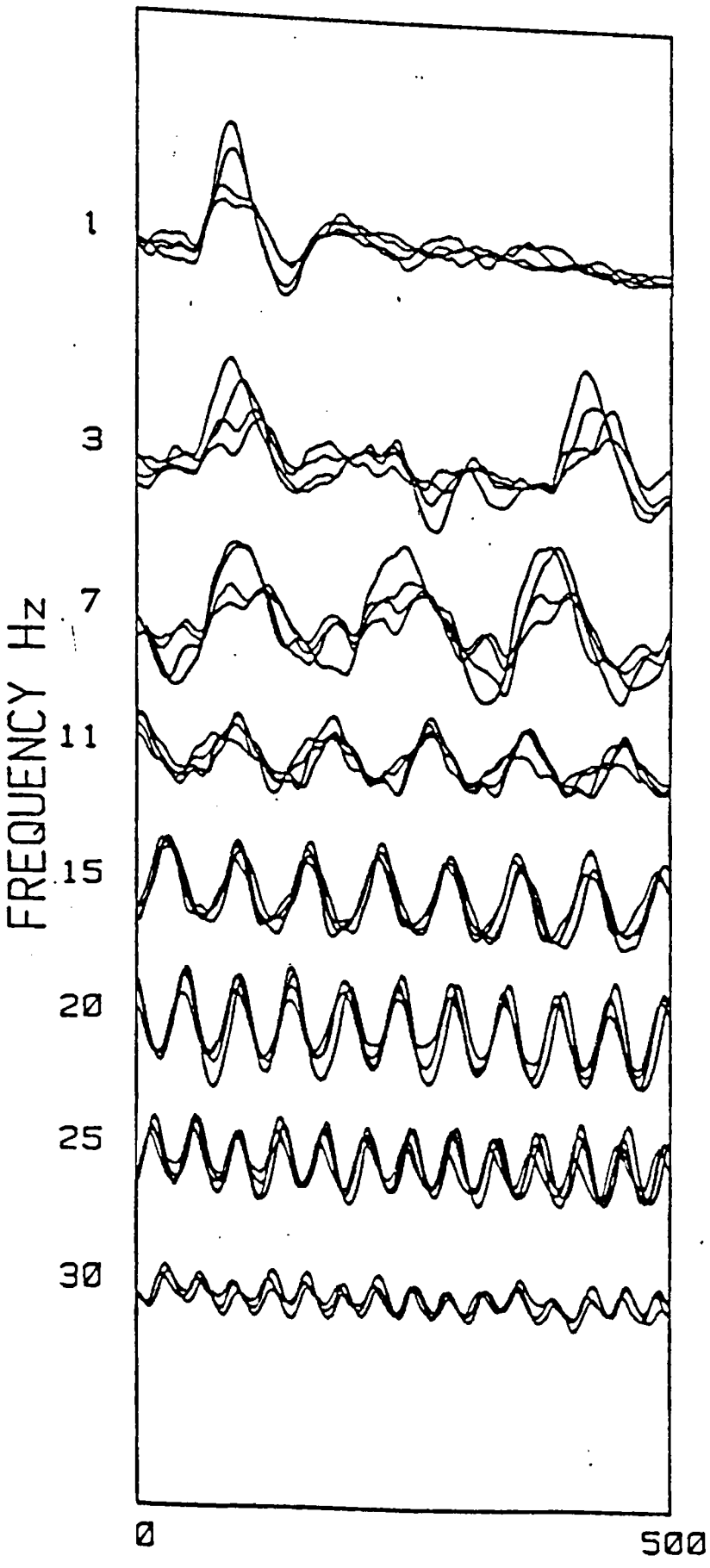


Figure 6.10c

Superimposed VEPs elicited by each of the four contrast squares. These VEPs indicate the consistency of and the small latency differences between different size squares. See text for discussion.

Square size (min arc)	Type	Peak latency (msec)
9	■ □	88 108
24	■ □	88 112
42	■ □	79 112
54	■ □	79 117

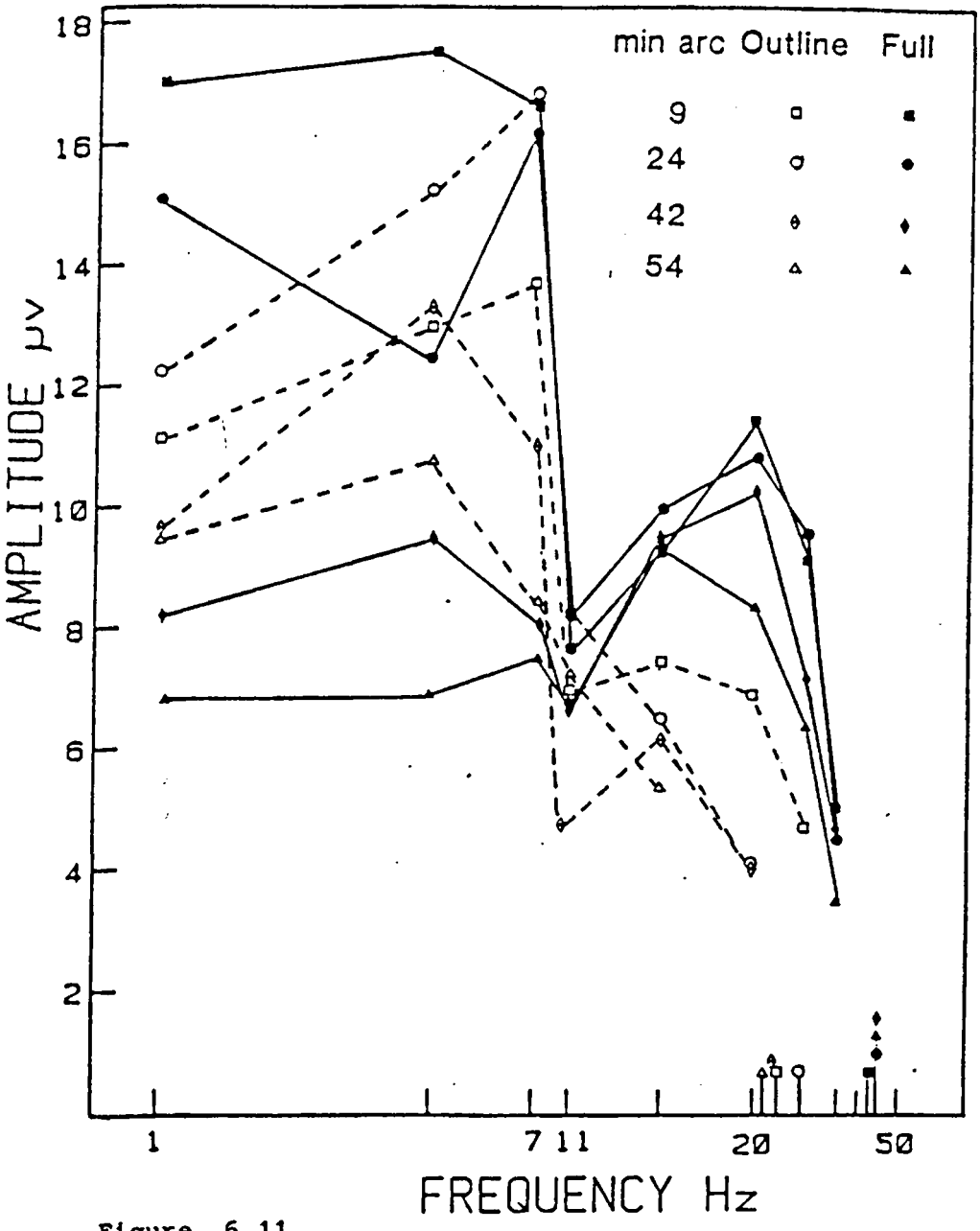


Figure 6.11

Values of peak latency differences of VEPs elicited at 1 Hz for contrast squares and outline squares of variable size. Also plotted are the mean peak-to-peak voltage elicited by outline squares (dashed trace) and contrast squares (continuous trace) for a range of square sizes. The psychophysically determined CFF is shown by the appropriate symbols on the abcissa.

Full symbols = contrast squares.

Open symbols = outline squares.

secondary peak to the contrast squares will temporally coincident with that of the outline square VEPs. The VEPs elicited by contrast squares of 9-24'arc have only a single peak, the latency of which is longer than that elicited by either the 42' or 54'arc squares, (see figures 6.12e & 6.13).

The phase difference between high frequency VEPs to outline and contrast squares are progressively reduced with decreasing square size, a feature explained by the fact that the peak latency of VEPs elicited by full contrast squares increases with decreasing square size, whilst the outline response will have a more constant latency.

The latency differences between high frequency potentials evoked by outline and contrast squares remain constant up to the limit of temporal resolution for the former. However because the latency of the VEP to outline squares is independent of sqaure size, which is not the case for the contrast squares, the latency difference between contrast squares and outline squares will differ as a function of square size. This, therefore, is further evidence that the properties of these high frequency VEPs are similar to that observed for CI under transient pattern-onset stimulation.

In figure 6.11 the mean peak-to-peak amplitude of the 500 msec sample, has been plotted as a function of temporal frequency and at the baseline are indicated the subjective CFFs for each of the stimulus patterns. As expected, CFF for contrast squares is higher, by some

threshold attenuation reported in psychophysical studies of TMTF have found this effect to be limited to stimuli of low spatial frequency.

The negative dip at 11 Hz may reflect some inhibitory activity, though in this case of a cortical origin, since it is maximal for small outline or contrast squares. Alternatively, these biphasic slopes may indicate the operation of two distinct mechanisms, the high frequency mechanism peaking at around 20 Hz and the dip in the curve reflecting a possible 'crossover' point between these two channels. If this is the case then it would appear that large squares are relatively more effective in evoking activity within the high frequency response mechanism than they are in the low frequency one.

The slopes of the hypothesised high frequency response mechanism when extrapolated to the baseline predict closely the psychophysical CFF for contrast squares. The correlation for outline squares response amplitude and psychophysical CFF is less exact, indeed they would appear to predict more clearly CFF for contrast squares. The dissociation between VEP amplitude and subjective sensation might be explained by assuming that the detection of contour involves mechanisms other than those operative at the level of the striate cortex; ie those contour specific mechanisms in the region of cortex which generates CII, or in 'higher' cortical regions.

6.6. General Discussion

The experiments reported here have attempted to provide electrophysiological data comparable to that reported in chapter 4, on the spatial/temporal properties of the retino-cortical pathways in man, in this case however, under steady state conditions, that is, under conditions which allow the system to adapt to a steady level of input. The results of experiments 6.1 and 6.3. have shown that resolution under such conditions is significantly better than that obtained with discrete pairs. The electrophysiological data were found to be quantitatively similar to the psychophysical data obtained under similar conditions and it is suggested the the two measures reflect aspects of the same mechanisms.

In light of previous studies (Cavonius & Sternheim,1972), this result was perhaps to be expected. However VEPs are not unitary phenomena and experiments were conducted which have attempted to

determine whether these high frequency VEPs obtained to pattern onset, reversal and luminance onset stimulation have a retinotopic selectivity and scalp distribution consistent with the prediction that the former mode of stimulation produced activity in the same region of visual cortex which generates the CI component of the transient pattern onset VEP.

The results have further shown high frequency pattern-onset VEPs are evoked only by the stimulation of those regions of the field which maximally evoke the CI component. This is consistent with the notion that they are indeed evoked by mechanisms within the same region of cortex. Although of course this does not imply that they are reflecting the same type of physiological activity, merely that this activity is localised to the same cortical region. Cells responsive to transient stimulation may be unresponsive to high rates of afferent input.

A feature commonly reported in early studies of the effects stimulating the receptive fields of single cells with flickering stimuli was that CFF, as measured by threshold response level, decreased as the number of synaptic stations increased. If the CFF for retinal neurons is 40 Hz, that of comparable geniculate neurons will be 30-35 Hz and the CFF for cortical neurons will be between 12-20 Hz (De Grand,1973), Geniculate neurons can however be driven at high temporal frequencies when their afferent fibers are electrically stimulated (De Grand,1973) suggesting that temporal resolution is determined by inhibitory neuronal connections.

Kimura (1981) has however reported, that in the cat, simple and complex type cortical cells respond to flickering stimuli up to frequencies of 15-60Hz. The discrepancy between these data and those reported by Grusser & Creutzfeldt (1957) appears related to the fact that the latter had used full field stimulation, whereas Kimura used slits and bars optimally positioned to give maximum responses at low temporal frequencies.

It was observed that the CII component, which Jeffreys (1977) has suggested does not contribute to pattern-reversal VEPs, also appears not to contribute to pattern-onset VEP at stimulation frequencies of above 5 Hz. Such a finding is consistent with the known properties of CII since the contour specific mechanisms that generate this component are adapted even with transient stimulation when stimulus durations are long (150 msec) relative to the inter-stimulus interval, (see

Jeffreys,1977). If these results hold for other subjects then it is evident that studies of high frequency pattern onset VEPs would benefit by choosing electrode positions and stimulating those regions of the visual field which are optimal for recording the CI component.

The third major finding is related to the responses obtained to flickering stimuli presented over a limit period of time, ie a flicker train. Pieron (1963) has suggested that the poorer resolution of brief pairs of stimuli as opposed to continuous trains is due to the unique response elicited by the first stimulus of the pair, which limits resolution by having a longer time course or by pushing the system into the region of saturation. The data presented in section 6.4 shows that this is indeed the case, and that the onset of a flicker pattern train does produce a response that is unique with regard to the others in the waveform. For intermittent trains, the limit of resolution appears lie between 25-30Hz, which is equivalent to an SOA of some 40-45 msec; a value close to that reported in chapter 4 for brief discrete pairs. This data is therefore consistent with Pieron's explanation of the poorer psychophysical resolution of such stimuli. Curiously this effect is limited to VEPs evoked by pattern stimulation; the first stimulus of the luminance modulated train either produces no response or one that is smaller than subsequent ones. The waveforms obtained suggest that luminance VEPs are similar to the output of a resonance filter, as reported by Van der Tweel & Lunel (1964). Thus again, there are clear distinctions between high frequency pattern and luminance VEPs.

That the VEPs elicited by such luminance stimuli are independent of retinal location and are approximately 180 degrees out of phase with similar frequency pattern-onset VEPs, further suggests that they have a different source locus. It is possible that the locus is not cortical and that these VEPS may indeed reflect sub-cortical activity because a general feature of the overall organisation of the visual system is that the more distal a cortical body from the peripheral receptors the more complex and specific are its functional properties. Thus, luminance modulated stimuli would evoke little if any activity in cortical regions having cells with a spatially opponent receptive field organisation. Indeed this conclusion must be drawn on the basis of the a comparison of the data of Grusser & Creutzfelt (1957) and Kimura (1981).

The final experiments indicated that the stimulus specificities of high frequency pattern VEPs are similar to those of the CI component;

specifically, it was shown that the latency or phase of the response to outline squares was independent of square size. This relationship does not hold for contrast squares, as the latency, phase, of the response is a decreasing function of square size, consistent with those of CI elicited by transient stimulation.

The properties of these high frequency VEPs can be explained in the following way. It is known that in monkey there exist two types of cell with differential function, the so called 'Tonic' and 'Phasic' classes (DeMonasterio et al,1975). It is known that the latter class have large receptive fields and a more transient and shorter latency response. Thus they are capable of following high temporal frequencies. The Tonic class, as reported in chapter 1, with smaller receptive fields, are concentrated in the fovea, have colour opponent receptive fields and are capable of following changes in stimulus wavelength at low temporal frequencies but their receptive field antagonism changes to synergism at higher temporal frequencies (Zerenner & Gouras,1980). Unlike the Phasic class they project predominantly to the parvocellular layers and not the magnocellular layers of the lateral geniculate body. At low temporal frequencies, stimuli of small angular subtense will predominantly evoke activity within the tonic class, the larger amplitude of the potentials elicited by smaller square patterns presumably reflecting the greater number of contrast borders within these stimuli. The smaller amplitude of the VEP to contrast squares at low temporal and spatial frequencies, relative to that of the outline squares would reflect the potency of contour for the tonic class with their small receptive fields. With increasing repetition rates, those mechanisms within striate cortex optimally stimulated by contour become less responsive, possibly as a result of inhibition. At the retinal level some of the phasic cells show synergism at high rates of stimulation and lose their colour opponent properties. It is possible that those mechanisms underlying the contour specific component of CI behave similarly and thus the contribution of this 'channel' to the overall level of activity within the visual cortex will be lessened The VEP will, at this point, be dominated by input from the ~~tonic~~ phasic class which with their larger receptive fields are capable of integrating contrast over a larger region of visual space.

Chapter 7:- Electrophysiological study of 'sustained' and 'transient' processing channels

Introduction

In recent years certain psychophysical data have been explained in terms of the activity of two distinct types of visual processing channels, the so called 'sustained'/'transient' systems (Kulikowski & Tolhurst,1972; Tolhurst,1975; Breitmeyer & Ganz,1976 Breitmeyer,1979; see also Lennie,1980 see also chapter 1).

A common assumption made by some workers is that the neuronal substrate of these channels are the 'X' and 'Y' type cells which have been reported extensively in the cat (see chapter 1). Because of the important role played by the concept of 'sustained' and 'transient' channels in some current theories of visual information processing (see for example Brietmeyer & Ganz,1976; Coltheart,1980; Stone et al,1980), it is important to examine whether there is indeed any electrophysiological evidence of such channels in the human visual system. In the experiments reported in the chapter I have attempted to do this by comparing the effects of stimulus duration, spatial frequency, configuration and contrast on the properties of the CI component.

There are two types of psychophysical data for which VEP correlates of the type associated with 'sustained' and 'transient' channels would be predicted. The first of these two, reported by a number of workers (Breitmeyer & Ganz,1975; Breitmeyer,1977; Harwerth & Levi,1977; Vasilev & Mintov,1976; Luppe et al,1976) has been the finding that both human and monkey (Harwerth et al,1977) reaction times (RT) to the onset of briefly presented sine and square wave gratings tends to increase as a function of increasing spatial frequency. The absolute value of this increase, per Log unit increment in spatial frequency, varies between studies; due perhaps to differences in experimental paradigms.

In one of the earliest studies of this type, that of Breitmeyer (1975), reported an increase of 100-150 msec in RTs to briefly presented sine wave gratings of frequencies of between 0.5-11cpd presented at a contrast of 0.5. Vasilev & Mintov (1976) similarly used

gratings of constant physical contrast and reported increases in RT latency of 43-56 msec over a spatial frequency range of 2-9 cpd. Lupp et al (1975) also report, in a more detailed study of stimuli with constant suprathreshold contrast, a latency increase of approximately 100 msec for a range of sine wave gratings of between 1-16 cpd. This value was moreover independent of suprathreshold contrast, in contradiction to the results of Vasilev & Mintov (1976).

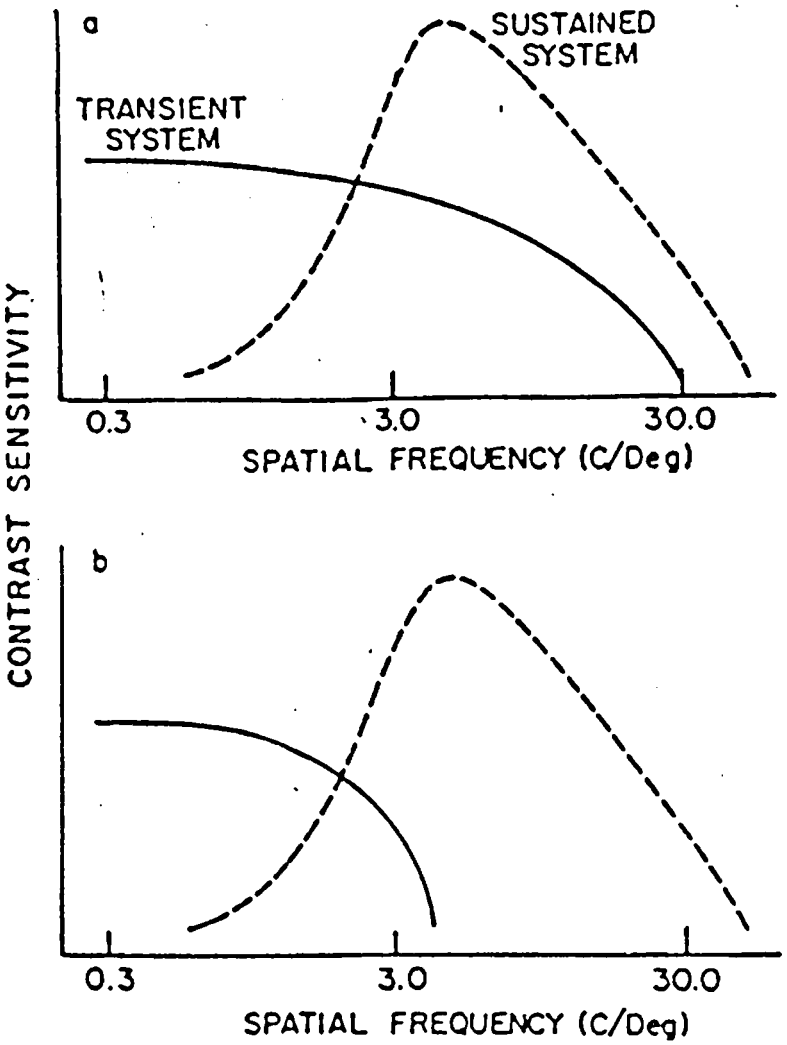
The conclusion reached by each of these studies was that the observed increase of RT's were consistent with the hypothesis (Kulikowski & Tolhurst,1973) that stimuli of high spatial frequencies are detected by a 'sustained' ('X' cell) system with a longer time course and response latency, and that lower spatial frequencies are processed in a separate, coarsely tuned but rapidly responding, (short latency), transient ('Y' cell) system. However Lupp et al (1975) offer an alternative explanation, noting that higher levels of cortical processing may be involved, since a fundamental principle of signal detection theory (Pike,1973) is that a more difficult discrimination takes a longer time. If the processing of detailed information, such as that contained in high spatial frequency gratings, involves more and/or a greater complexity of neural interactions within visual cortex this could account for the observed increase in RT. This explanation appears to have been overlooked by other workers.

If transmission times within the primary visual pathway are indeed the main factor contributing to these latency increases they are, of themselves, not direct evidence for two distinct processing channels, since the slope of the RT v spatial frequency function are, in each case, linear, whereas a biphasic function might perhaps be predicted (Parker & Salzen,1977). This has been reported by Harwerth & Levi (1977) in experiments which measured reaction times to briefly presented gratings of variable contrast and frequency. The underlying assumption of the experiment was as follows. Because single unit data have suggested that 'Y' type cells have large receptive fields and short response latencies, whilst the 'X' type cells have smaller receptive fields and longer response latency and time courses, it seems likely that high spatial frequencies would be processed by 'X' cells, and low frequencies by 'Y' cells. However there should be a limited range of intermediate frequencies for which both types of cells (channels) would be sensitive. Harwerth & Levi further predicted that the 'transient' channel would be optimally stimulated at high contrast levels whilst the 'sustained' ones would respond optimally at low contrast because of

Figure 7.1

From Harwerth and Levi (1977). and Harwerth et al (1978). Reaction time plotted as a function log contrast for stimuli of variable spatial frequency. At frequencies of between 2-8 cpd the latency functions appear to be bimodal which is not the case for frequencies higher or lower than this. These authors argue that the 'kink' represents the point of change from a transient to a sustained processing system.

Similar function are reported for monkey (fig 7.1b) and are absent from the abnormal eye of the amblyope. See text for discussion.



Schematic representation of the spatial frequency tuning of the sustained and transient mechanisms. Top panel shows sensitivity of the two mechanisms as proposed by Kulikowski and Tolhurst (1973). Relative sensitivities suggested by Legge (1978) are shown in the bottom panel.

Figure 7.2

Spatial properties of transient and sustained channels as hypothesised by Tolhurst & Kulikowski (1972) and Legge (1977).

their greater temporal integration. The data presented in figure 7.1 (Harwerth & Levi,1977) suggests that these assumptions have indeed been justified since the reaction time functions are bimodal for frequencies between 2-8 cpd, but not for higher (12 cpd) or lower (0.5 cpd) frequencies. The absolute value of the latency increase as a function of spatial frequency observed in this study amounted to 80 msec, even at high (0.45) contrast levels, a value intermediate therefore between that reported by Breitmeyer (1975) and Lupp et al (1976).

Harwerth et al (1978) have further shown that in the amblyopic subject, bimodal RT functions obtained for stimulation of the normal eye are not seen when the stimuli are restricted to the abnormal eye, (see figure 7.1c). They suggest therefore that the primary impairment to visual function in amblyopia is 'damage' to 'sustained' visual channels, since the RT's are shifted to higher values; a suggestion first made by Ikeda & Wright (1974) on the basis of single unit studies of the cat.

The second line of evidence suggesting the existence of two distinct processing channels has been provided by the examination of temporal integration as a function of spatial frequency (Legge,1977; Nachmias,1968; Breitmeyer & Ganz,1977). The latter had measured spatial frequency thresholds as a function of stimulus duration for sine wave gratings between 0.5, 2.8 and 16 cpd. They reported that at durations between 20-400 msec threshold progressively drops to some critical duration which is dependent on spatial frequency, being 50 msec at 0.5 cpd and 200 msec at 16 cpd. The data of Nachmias (1967) has similarly been interpreted as indicating the existence of 'sustained' and 'transient' channels. Nachmias had reported that contrast threshold for 0.7 cpd square wave gratings remained constant at durations above 50 msec but continued to fall for gratings of 17 cpd, up to presentation times of 500 msec.

Legge (1977) has provided more comprehensive psychophysical data purportedly characterising the spatio-temporal properties of these postulated channels. He reports that contrast thresholds for sine wave gratings of 1.5 cpd, and above continue to fall with increasing presentation times up to durations of 1000 msec. The slope of the curves were triphasic for frequencies above this value, with a fairly sharp decline up to 50-100 msec, beyond this value the slopes shows a more gradual decline. For frequencies less than 1.5 cpd the slope of the threshold function also shows a sharp decline up 100 msec but

thereafter levels off, becoming independent of presentation time. Legge has argued that such functions reflect the activity of two distinct channels, although it should be noted that the high frequency cut-off of his 'transient' channels are a good deal lower than reported by Kulikowski & Tolhurst (1973), and illustrated in figure 7.2.

7.1:- VEP evidence of 'sustained/transient' channels'

Electrophysiological data, in the form of the VEPs, have also been presented in support of some of the above psychophysical data. For example, Vassilev & Strashimirov (1977) report that the latency of VEPs to the onset of sine wave gratings increased by some 120 msec over the frequency range 1-16 cpd, the short latency response being attributed to the activity of 'transient' cortical cells. Jones & Keck (1979) report similar effects and claim to have identified a peak specifically reflecting transient cortical cell activity. Unfortunately, their conclusion that the 'transient' pattern-onset VEP consists of a relatively simple waveform is inconsistent with the conclusion of the detailed studies of Jeffreys & Axford (1972). [There are at least six identifiable components in pattern-onset VEPs, three of these which appear to originate from separate retinotopicaly organised regions of cortex and, unlike the other three, are pattern specific, (Jeffreys & Musselwhite, in prep)].

However each of the above studies failed to show that the peaks

a:- reflected only pattern specific activity

b:- had a scalp distribution and polarity consistent with the current models of the visual field representations within striate or extrastriate cortex of man.

and finally

c:- were the same components in each of the subjects studied, Little credence can therefore be given to their conclusions.

A similar conclusion must be drawn with regard to the studies of Parker & Salzen (1976; 1977). They reported latency functions for VEP components defined in terms of their peak latencies. Over a range of frequencies from 0.5-10 cpd, a latency increase of 60-70 msec was obtained. The slopes of these curves were monotonic and thus they interpret the increase as reflecting a spatial frequency specific increase in conduction velocity within a single ('X','sustained') channel.

Part I

7.2:- Experiment 1:- VEPs elicited by sine and square wave gratings

In this experiment I examine the effects of contrast and spatial frequency on the latency and amplitude of CI for stimuli with sine and square wave contrast profiles. It has been proposed by Legge, (1977), that an adequate characterisation of the properties of the sustained/transient channels can only be determined by the use of sine wave stimuli which lack higher harmonics. In the experiments to be reported later in this chapter an examination of the effects of spatial frequency and element size on the properties of the CI component will be undertaken with sharp edged contrast stimuli. It is important therefore to determine whether there are any differences in the properties of CI elicited by sine and square wave stimuli since if there are this will affect the conclusions and the implications that can be drawn from following experiments with regard to the theories outlined in the introduction to this chapter.

Procedure

Stimuli were presented on the face of Hewlett-Packard (1300A) X-Y display according to a modified method of Campbell & Green (1965). Stimuli were presented in the on-off mode for a duration of 100 msec which preliminary experiments had shown to be the most effective duration. Gratings of 0.5-11 cpd were produced by a function generator and their contrast adjusted by a calibrated potentiometer. A small, continuously illuminated LED, positioned in the centre of the screen, provided a fixation point.

A single subject participated and the stimuli were presented to the left half field, the right field being occluded by a field stop. A viewing hood of 59 cm length was attached to the front of the X-Y display producing a viewing angle of 1 degree for every 1 cm. The overall luminance of the field was $30cdm^{-2}$. Five runs of 30 sweeps at an aperiodic interstimulus interval of some 1200 msec were undertaken for each stimulus condition. At each spatial frequency, contrast was set to one of nine predetermined values before changing to either a new setting or different contrast profile. This procedure was chosen in preference to a more random design in which contrast, spatial frequency

and contrast profile were simultaneously varied, because of ease and rapidity.

Results

In figure 7.3 are shown typical waveforms elicited by stimuli of variable spatial frequency, contrast and contrast profile. These waveforms indicate that there is little difference between the form of the VEP elicited by either type of grating.

The effect of spatial frequency and contrast on the peak latency on this component have been shown in figure 7.4 where latency is plotted as a function of stimulus contrast for each of the frequencies used. Three features are evident.

Firstly, as spatial frequency is increased there is a systematic increase in peak latency which is approximately constant across the contrast range studied. A more detailed examination of the effects of spatial frequency on peak latency are reported below.

Secondly, the slope of the latency functions are apparently linear across the range for both sine and square wave gratings. There is some evidence that the slopes differ at the medium to high frequency range, but the difference is small and unlikely to be of functional significance. The actual increase per unit of contrast is similar to that reported for the N 70-120 peak elicited by sine wave gratings reported by Kulikowski (1979, see fig7.10 page 181).

It is not known however whether the VEPs recorded by Kulikowski reflect similar cortical activity to that of the CI component. Since he has studied in greater detail the effects of contrast and spatial frequency on VEPs elicited by sine wave stimuli it would be interesting to determine the exact relationship between his VEPs and the pattern specific components investigated here, which have been shown to have a specific cortical origin.

7.3:- Experiment 7.2:- Effects of spatial frequency on VEP latency

In this experiment the peak latency of CI were studied as a function of the spatial frequency of square wave gratings, briefly presented in tachistoscope A. Stimuli were again prepared from high contrast photographic transparencies. Three subjects participated.

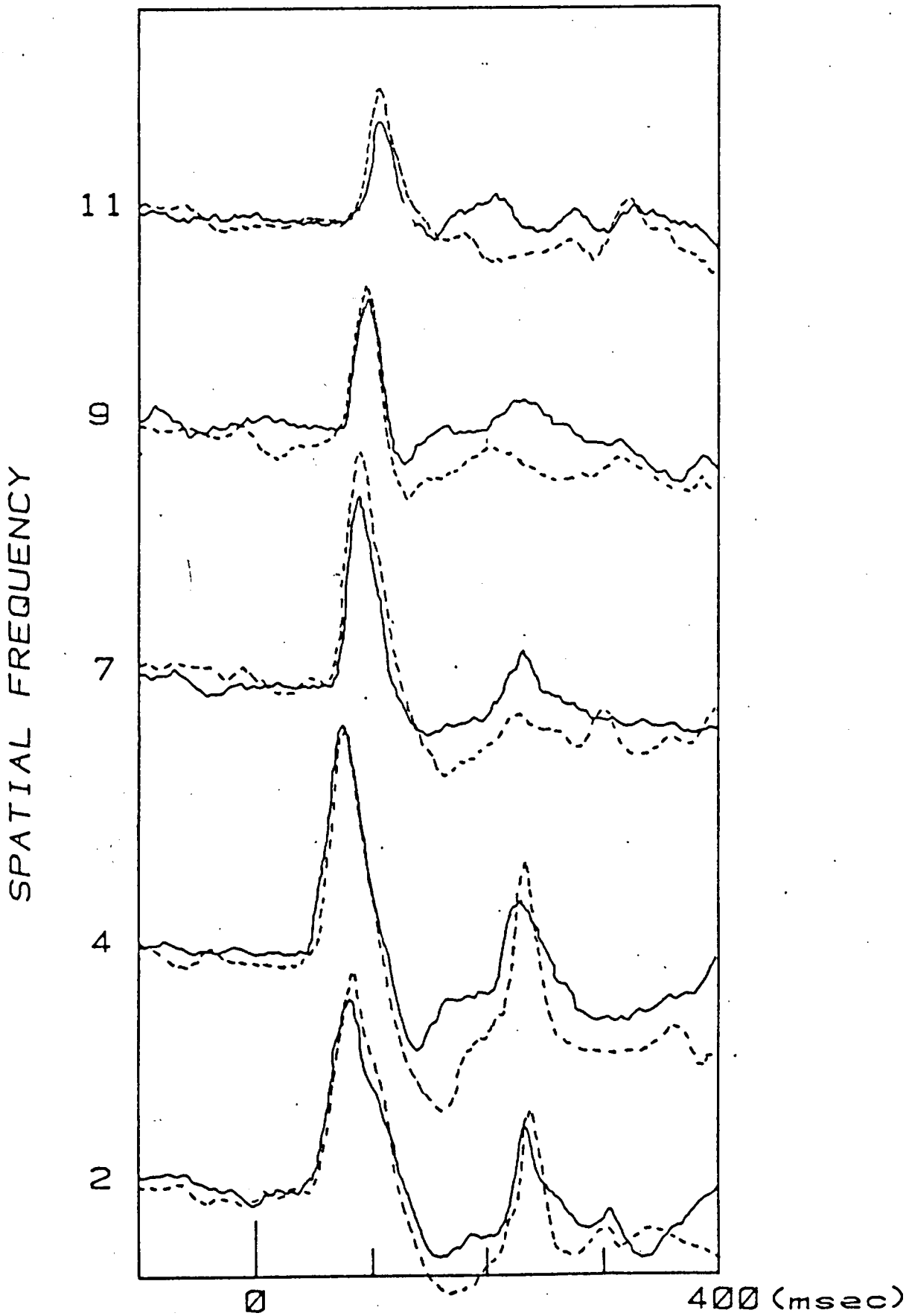


Figure 7.3

CI elicited by sine (full trace) and square (dashed trace) wave gratings.

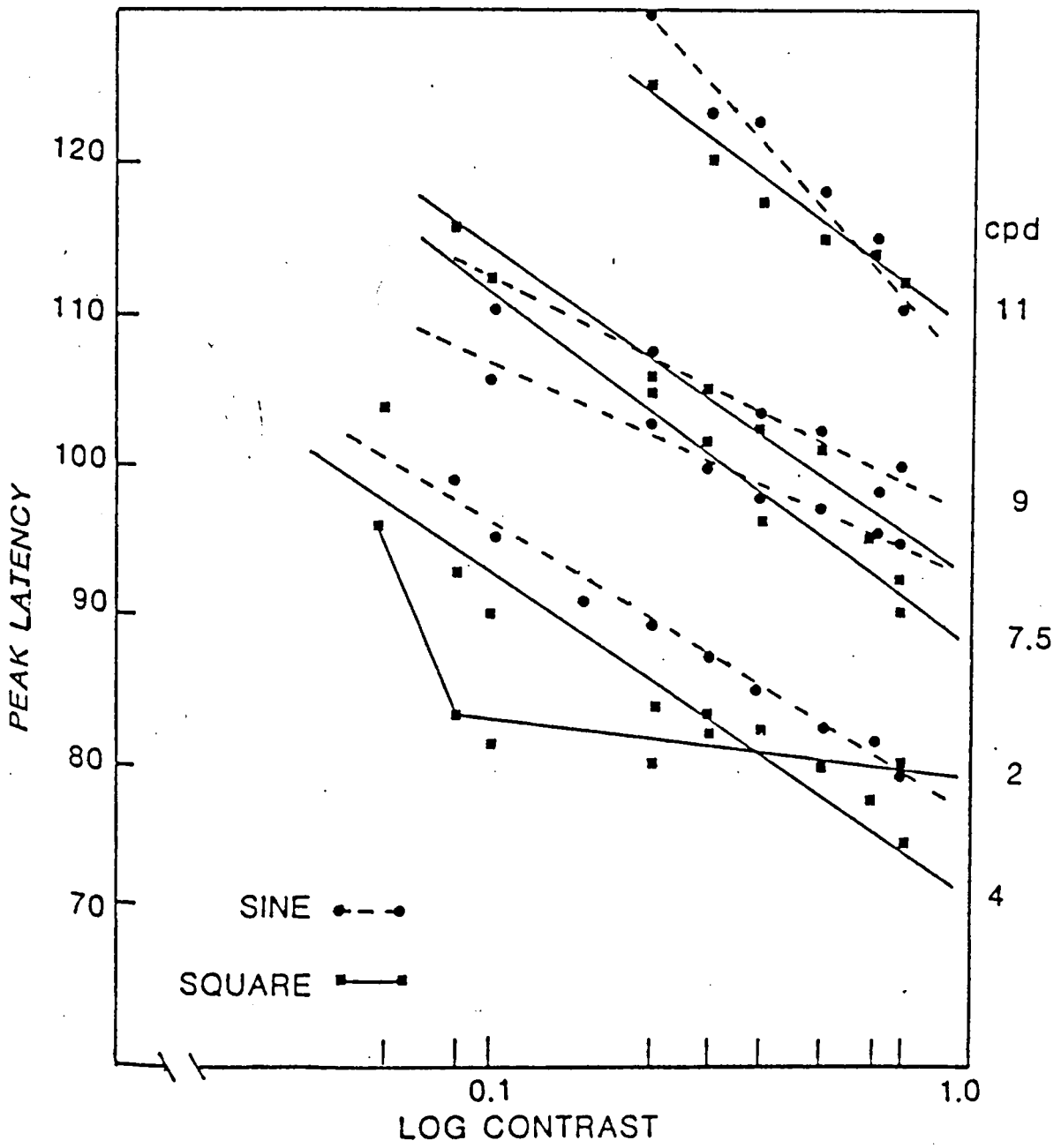


Figure 7.4

Plots of peak latency as a function of contrast for sine (●) and square (■) wave gratings of variable spatial frequency. Data are for one subject.

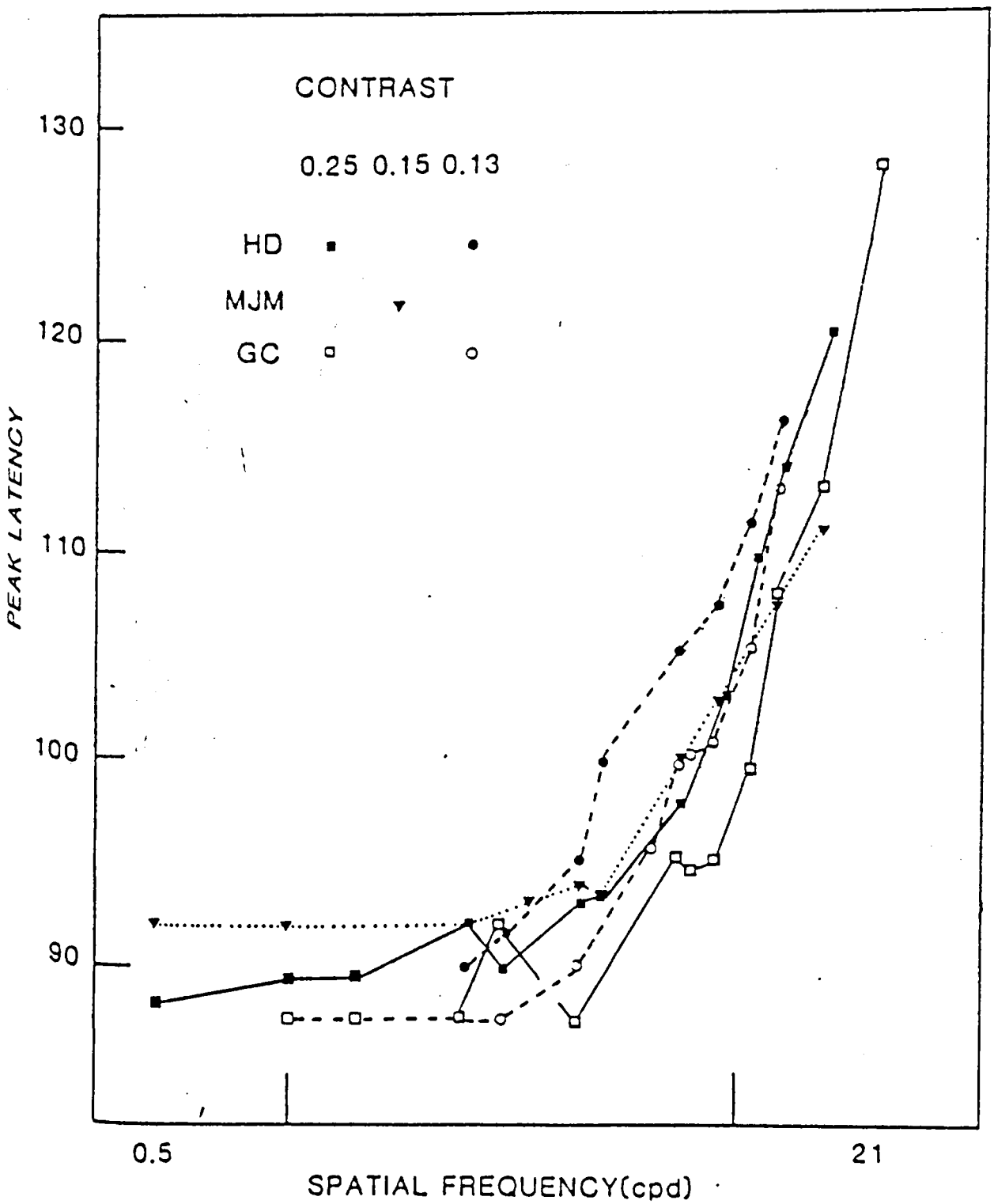


Figure 7.5
Plots of peak latency as a function of spatial frequency at two levels of contrast. Data are for three subjects.

Field size was 9 degrees and the stimuli were presented for 150 msec, a duration which allowed for the separation of 'off' and 'on' responses which might possibly interact at shorter durations.

Smith (1979,unpublished doctoral dissertation) has reported spatial-frequency dependent latency functions for all three pattern specific components, CI, CII and CIII to checkerboard stimuli. However in his study, sampling time was high (5 msec), and the stimuli presented at maximum contrast. CI saturates at about 50% contrast and it is probable ,that his data reflect an upper limit of neural transmission between retina and cortex, which may thus have masked any spatial frequency dependent latency increase. He also did not use optimal conditions to separate out the three component peaks.

Results

In figure 7.5 peak latency has been plotted as a function of spatial frequency from 0.5-21 cpd. Two features are evident. Firstly peak latency increases as a function of spatial frequency consistent with the results of experiment 7.1. The overall increase from the lowest to highest frequency used being some 30 msec. Secondly there is a distinct latency 'saturation' at low spatial frequencies; with increasing frequency, the peak latency increases approximately linearly.

7.4:- Experiment 7.3:- Effects of stimulus type on VEP latency

Previous experiments have shown that the peak latency of CI is spatial frequency dependent. Preliminary experiments had also suggested that in addition to spatial frequency, or stimulus element size, stimulus configuration was a further variable of influence on peak latency. In the following experiment the effects of stimulus size and type on the latency of CI at both constant and variable contrast levels are systematically examined. The question being asked here is, what are the relevant spatial parameters that determine the latency of cortical activity ?.

Procedure

All stimuli were high contrast photographic transparencies (gratings, isolated square patterns and checkerboards) presented to the left half field for a duration of 150 msec.

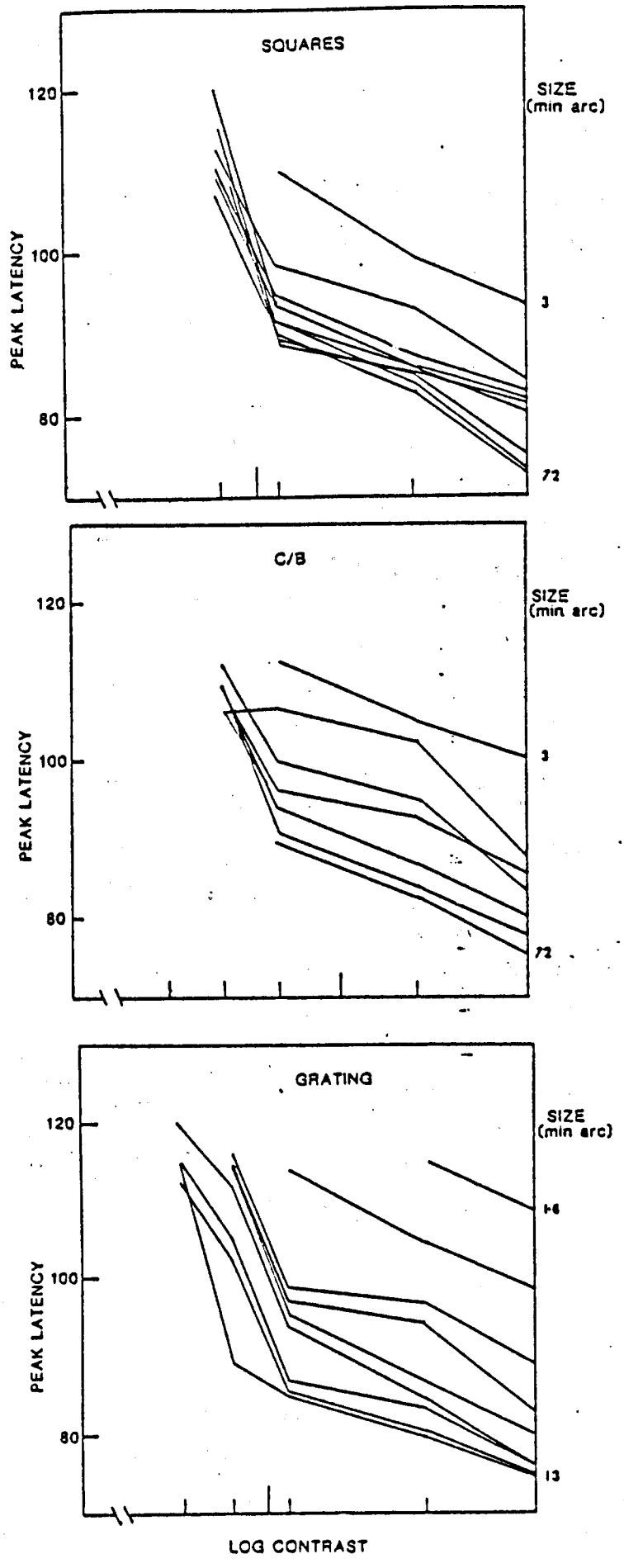


Figure 7.6

Plots of peak latency as a function of log contrast for three stimulus types. For clarity data points have been removed.

Results & Discussion

The peak latency of CI elicited by the three stimulus types has been plotted as a function Log contrast in figure 7.6. For clarity of presentation only a limited number of data points have been shown. Two features are evident.

Firstly, as contrast is systematically reduced peak latency progressively increases, consistent with previous data presented in this thesis.

Secondly, as element size is decreased, there is a progressive increase in peak latency, which is approximately constant as a function of contrast. The value of this contrast-dependent latency increase, depends on stimulus type. There is some evidence of bimodality in the latency functions, particularly for the isolated square stimuli, but it is unlikely to be of functional significance.

In figure 7.7 peak latency is plotted as a function of log element width for the differing stimulus types. A number of features are evident. Firstly, for a constant element size the absolute latency of response is dependent on stimulus type. Thus the latency of cortical response is shorter for gratings than for isolated squares which in turn are shorter than for checkerboards. Secondly, the functions are bimodal and there is a distinct kink in the curves at and around stimulus sizes eqivalent to the bar width of a 4-5 cpd square wave grating. For stimuli whose elements are larger than approximately 6-7'arc, the latency functions appear to be constant; for values smaller than this peak latency increases systematically with decreasing stimulus size, similar to the data of section 7.4. The knee of this function appears to shift toward larger element sizes as stimulus contrast is progressively reduced.

The overall latency increase observed for gratings is approximately 30 msec over a range of stimulus sizes, which in terms of spatial frequency, is between 0.5 and 20 cpd. The bimodality of this function is consistent with the suggestion that there are two underlying mechanisms carrying signals elicited by high and low spatial frequencies, and which could be interpreted in terms of the sustained/transient model. In order to test this assumption the following experiment was conducted. Field size was reduced, and gratings of variable frequency presented at three contrast levels of

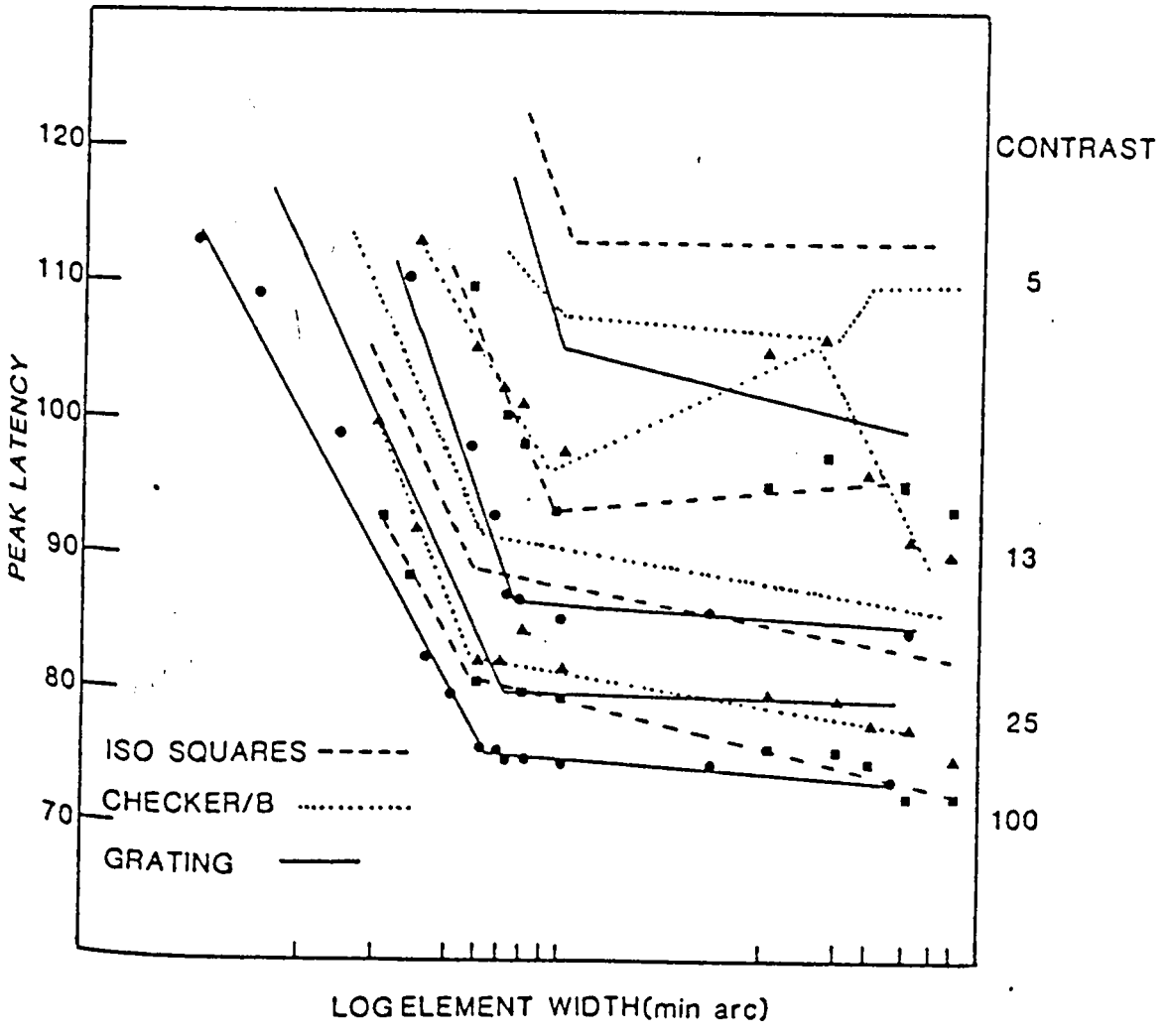


Figure 7.7

Plots of peak latency as a function of stimulus type and stimulus contrast. A limited number of points have been plotted, for clarity of presentation.

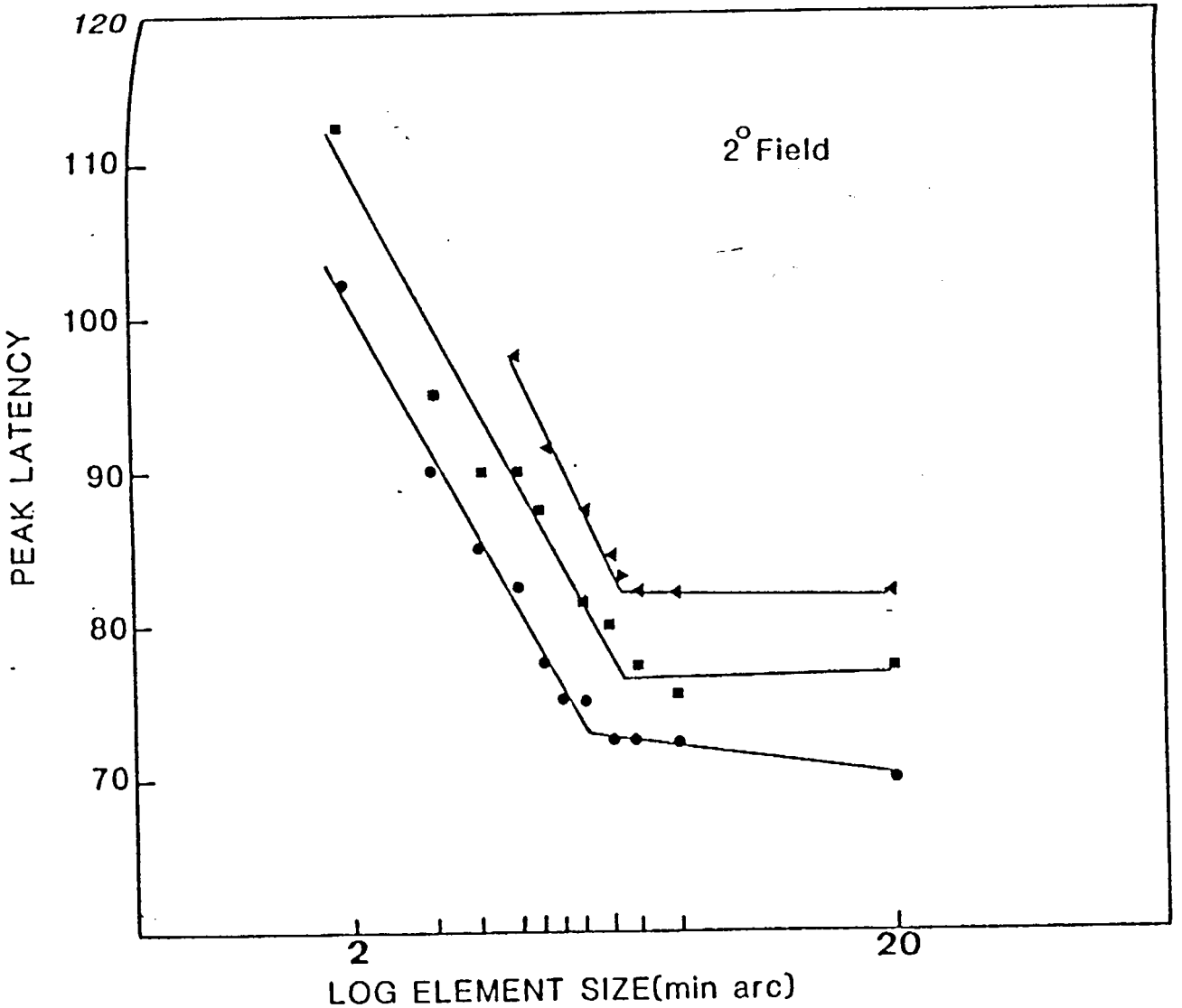


Figure 7.8
Latency of CI plotted as a function of log element size for a 2' field.

1.00, 0.25 and 0.13. It is argued that the sustained channels are confined to the foveal region (Breitmeyer & Ganz,1976; Breitmeyer,1979) where visual acuity is highest. If this is the case then it would be predicted that the latency function of CI should be unimodal.

An obvious problem here is that a reduction in field size produces a decrease in the number of grating periods so that the amplitude of the VEPs elicited by low frequency stimuli becomes little larger than noise level. This problem cannot reasonably be overcome under the present conditions.

Results and Discussion

In figure 7.8 peak latency is plotted as a function of element size. The main features observed in previous experiments are also evident here, that is, peak latency increases as a function of contrast and element size. Again there is a distinct kink in the latency function at around 6-7'arc (4-5 cpds in terms of spatial frequency). If the initial portion of the curve represents transient channel activity and the steeper portion, sustained channel activity, then the results suggest that transient channels must cover the fovea.

7.5:- General Discussion. Part I

The results of these experiments can be summarisd as follows.

a:- the peak latency of CI increases as a function of the spatial frequency of the evoking stimulus

b:- peak latency also increases as a function of decreasing contrast (as was also shown in chapter 3, the values being similar to that reported here). A combined decrease in contrast and increase in spatial frequency does not reveal any frequency-dependent bimodal latency function of the type decribed by Harwerth and Levi (1977).

An increase of spatial frequency at a constant level of suprathreshold contrast produces over the frequency range 0.5-21 cpd an increase in peak latency of some 25-30 msec. This size dependent latency increase is not however independent of stimulus type. Thus linear gratings will elicit VEPs of shorter latency than comparably sized isolated squares which will, in their turn, have a shorter latency than comparably sized checkerboards. At lower contrast levels, checkerboard stimuli elicit VEPs of shorter latency than isolated squares; it is not known whether this feature reflects the facilitatory

effects of the low frequency Fourier components of the former.

c:- sine and square wave gratings of equal contrast and frequency appear to activate the generators of this VEP component in a similar manner; the peak latency of the responses elicited by them are, within the limits of measurement, similar, (although the amplitude of the VEP elicited by sine waves are generally smaller). Subjectively, it is impossible with the brief presentation times used in this study to distinguish sine from square wave gratings above frequencies of approximately 4-5 cpd: similarly, psychophysical data have shown that their contrast sensitivities differ little above 4-5 cpd. The major difference occurs at the low frequency range where sensitivity to sine wave stimuli is lower than that for comparable square wave stimuli. Kelly has suggested that the mechanisms producing this effect are of retinal origin. Unfortunately, gratings of very low spatial frequency (1 cpd) do not evoke VEPs with a consistent signal to noise ratio and it was not thought worth the time and effort to examine VEPs to such stimuli.

Schiller et al (1977) have examined the responsiveness of single cells in monkey striate cortex to gratings of both sine and square wave contrast profile. They report that square wave stimuli of optimal spatial frequency and orientation are more effective in driving cells than gratings with a sine wave contrast profile. The latency of discharge appears however to be independent of the contrast profile. There is some evidence that the amplitude of CI also shows this relationship because the amplitude of the potential elicited by square wave gratings tends to be larger than that evoked by sine waves of comparable spatial frequency.

The present results question the suggestion of Legge (1977) that the use of predominantly 'sharp' edged stimuli such as square wave gratings and checkerboards (with high frequency components) will favour the sustained channels and therefore bias the data.

Moreover, in contrast to those of VEP studies in which sine wave stimuli of a limited frequency range have been used, these results have also shown that for CI, there are no large spatial frequency dependent increases in the peak latency. A latency increase of just 25-30 msec is observed over the frequency range 0.5-21 cpd. Vasilev & Strashimirov (1977) however, report a similar increase over the range 1-4 cpd, and Jones & Keck (1979) a comparable increase over the range 1-5 cpd. The increased latency of cortical activity reported by these workers must

either reflect components of extrastriate orgin (though this seems exceedingly unlikely) or, alternatively, reflect the combined interaction of pattern and non pattern specific activity and thus be unrepresentative of any single underlying physiological mechanism. Certainly it is unrealistic to assume that the latency increases observed in the above studies reflect solely increases in conduction velocity within the primary visual pathways.

The picture is complicated however by the data presented in figure 7.7; here the latency function appears to be biphasic when plotted as a function of element size, which would indeed be consistent with the notion that there are two distinct underlying pathways with differing spatial and temporal properties, the latter with an apparently constant response latency, optimally stimulated by large stimulus elements of greater than 6.0°-7.5°arc and the other with a size dependent response latency, operative at element sizes smaller than this. When contrast is reduced, the knee of the function systematically shifts toward larger element sizes. If size-dependent bimodal functions of this kind are indeed indicative of two underlying mechanisms of a type similar to that postulated by psychophysicists then this data would suggest that even at the maximal point the latency difference between 'channels' is only some 30 msec.

However some of the latency increase can be explained in the following manner. Now it is known that for both sine and square wave gratings human MTF shows a distinct peak at around 5 cpd (Kelly,1975). With continuous presentation, there is pronounced threshold attenuation of high frequencies, and also some attenuation of low frequencies, particularly for sine wave stimuli. High frequency attenuation persists when the optics of the eye have been bypassed (Campbell & Green,1965). VEP amplitude is also known to be stimulus size dependent at suprathreshold levels and to show a similar spatial frequency tuning (see Spekreijse et al,1977).

This electrophysiological phenomenon can be explained in terms of either the smaller number of cells tuned to the the high frequency range and/or to the fact that receptive field size increases with eccentricity; thus gratings presented within a constant field size will stimulate a progressively smaller region of visual cortex. This does not explain the increased latency of cortical activity as a function spatial frequency. However if the optical attenuation reduces effective contrast at high spatial frequencies then some of the observed latency

increase may be readily explained since peak latency has been shown to be a function of stimulus contrast.

This cannot be the whole story because the latency increase over the frequency range studied would be equivalent to a decrease in effective contrast of some 90 % and it is unrealistic to ascribe such a value wholely to optical attenuation. The spatial frequency dependent increase of peak latency is likely to be the result of either the increased time constant of the retinal mechanisms for high frequency gratings, and/or increased conduction time within the primary visual pathways. The overall values are however considerably lower than that reported by other workers.

PART II

7.6:- Experiment 7.5:- The effect of spatial frequency on the time course of temporal integration.

Procedure

In the following experiments the critical duration over which the amplitude of CI shows contrast/duration reciprocity will be examined as a function of spatial frequency for square wave gratings of between 1-10 cpd. The procedure was similar to that described in chapter 3.

Results In figure 7.9a-b the amplitude of CI has been plotted as a function of Log (contrast x duration) for each of the four gratings presented. A general feature is evident, this is that the points fall on or close to a straight line which, when extrapolated to the baseline, predicts the psychophysically determined duration thresholds at each level of contrast.

In figure 7.10 are shown comparable data for one other subject for a 6 cpd grating. Unfortunately the whole series could not be completed for this subject because of limitations of time (to conduct the whole series on one subject with breaks to counteract boredom took over 10 hours). However the general trend is the same. As was shown in chapter 3, contrast and duration are here reciprocally related at least up to duration of 50 msec and this effect is independent of spatial frequency.

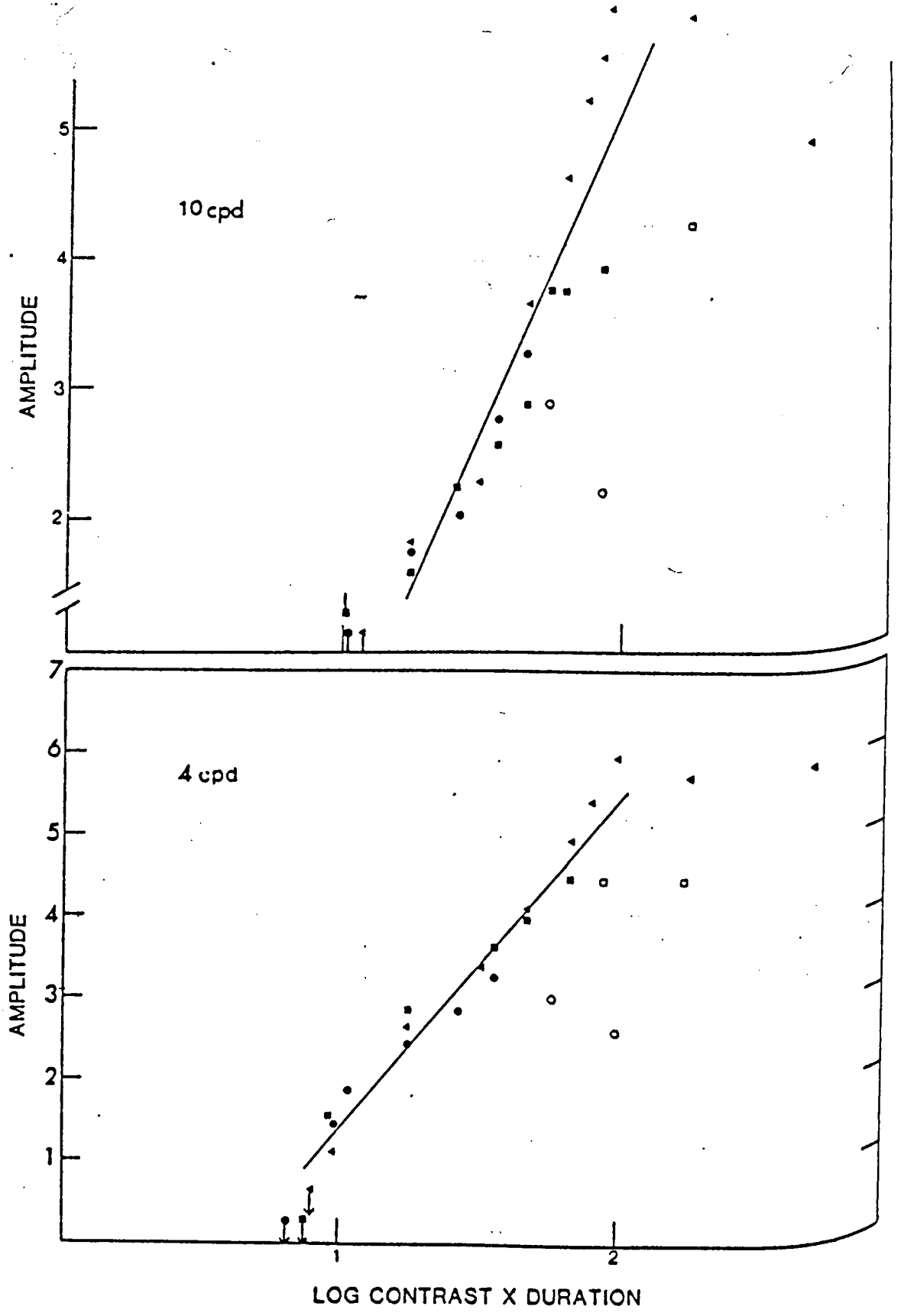
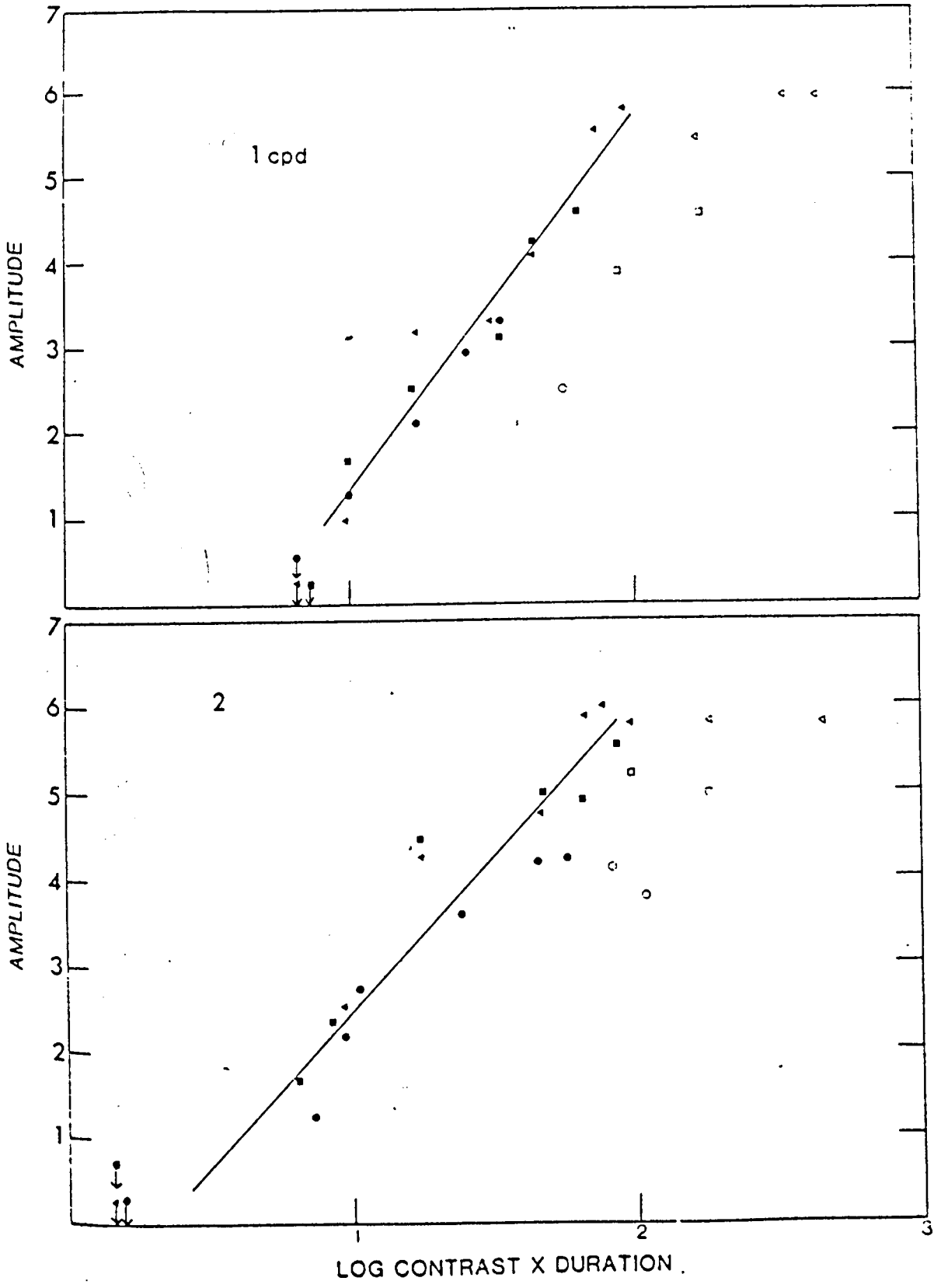


Figure 7.9a-b

Amplitude of CI plotted as a function of log (contrast x duration) at three levels of contrast 0.30 (◀), 0.15 (■) and 0.075 (●), for stimuli of four spatial frequencies.


1 cpd
2
AMPLITUDE
AMPLITUDE
LOG CONTRAST X DURATION

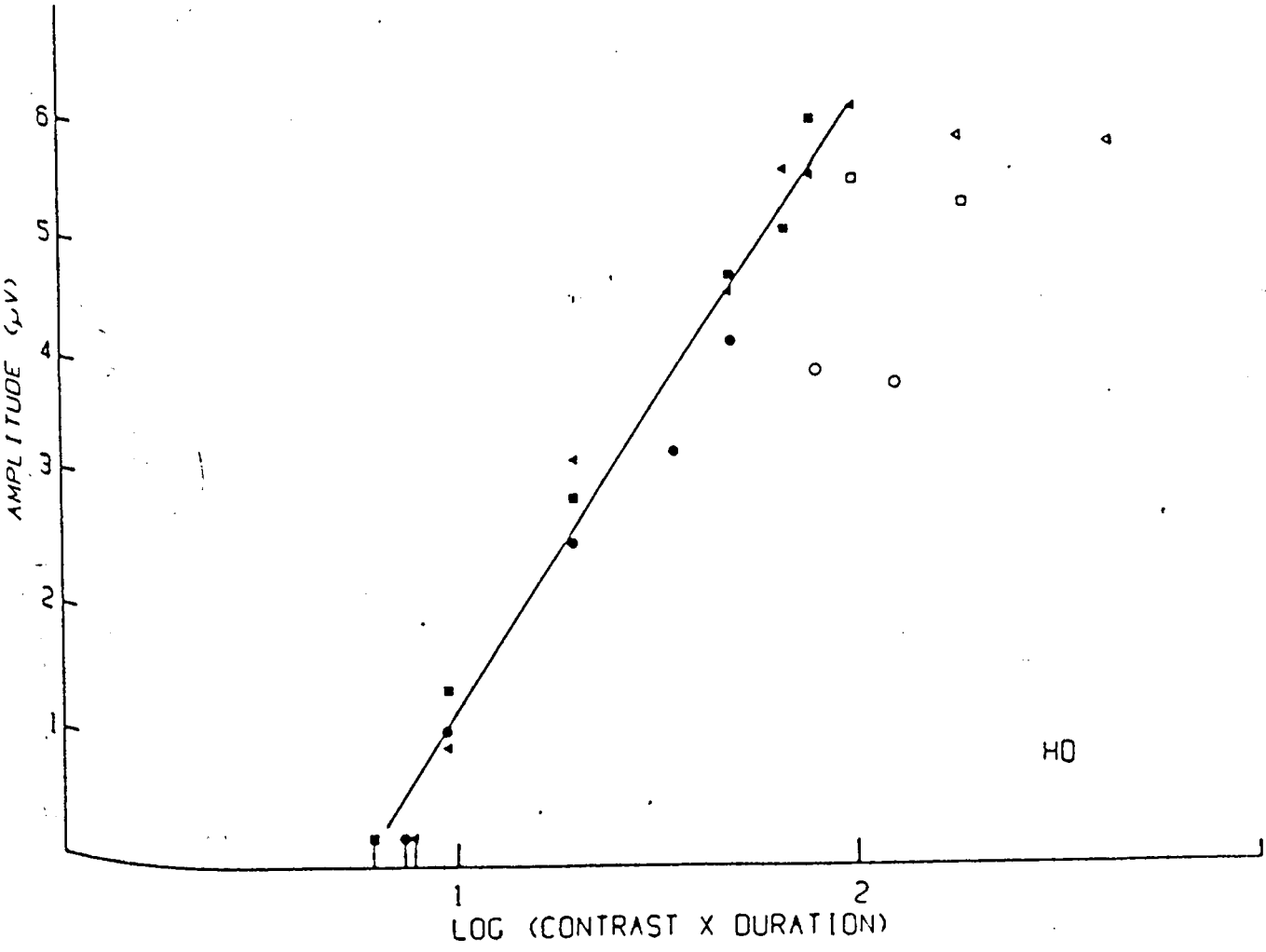


Figure 7.10
Plots of CI amplitude as a function of the Log (contrast X duration) product for a second subject. Stimulus was a 6 cycles/deg square wave grating.

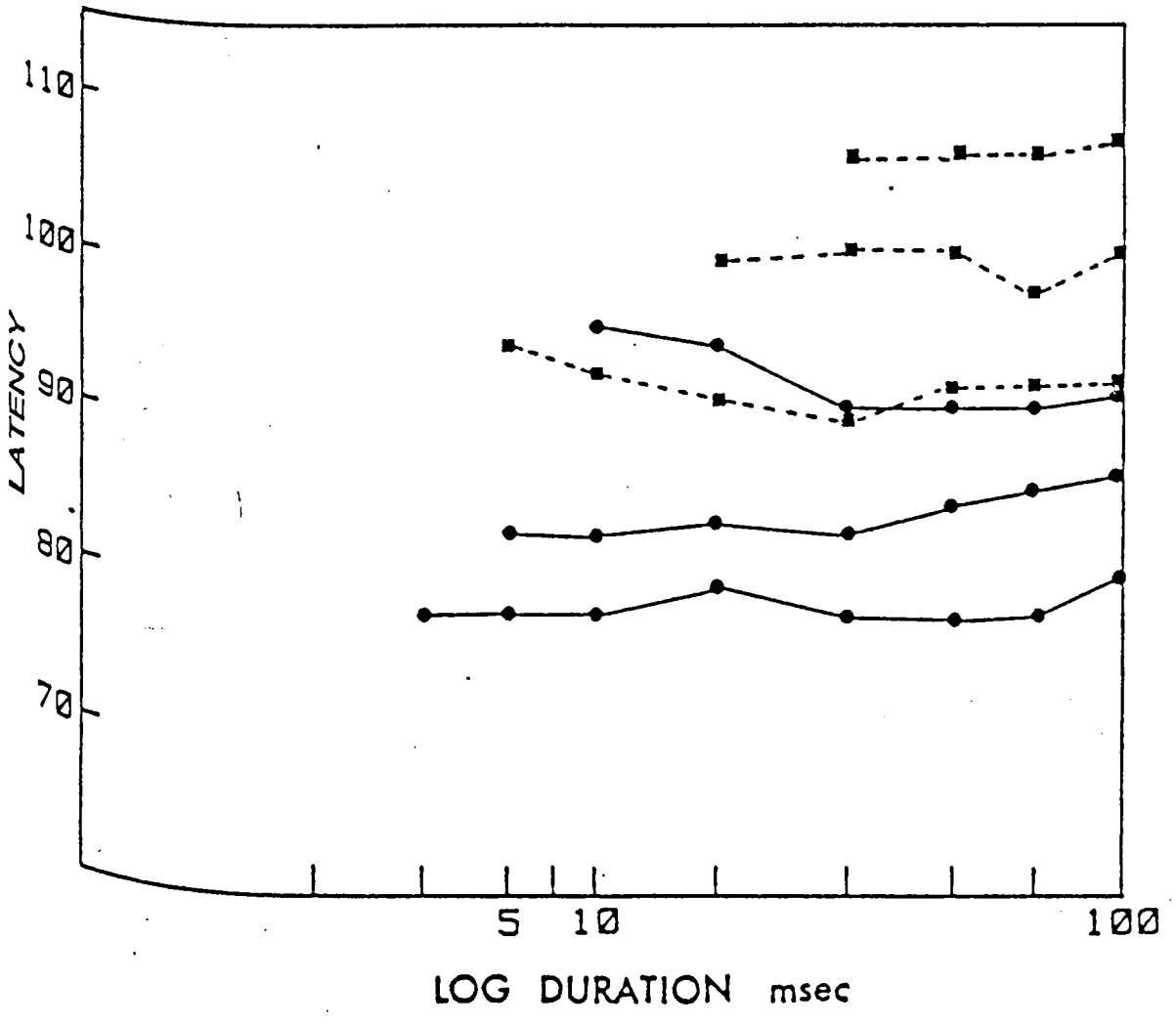


Figure 7.11

Plots of peak latency as a function of stimulus duration for stimuli of two spatial frequencies, (●) 1cpd, (■) 10cpd. At contrast levels of 0.30, 0.15 & 0.075.

The slopes of these curves do differ, being steeper at higher frequencies. It is difficult from such a limited study to determine the significance of this effect. Duration thresholds are higher at high spatial frequencies, consistent with the psychophysical data. In figure 7.11 the latency of CI is plotted as a function of stimulus duration at each of the three levels of contrast for the highest and lowest spatial frequencies studied. The independence of peak latency and subjective contrast is similar to that reported in chapter 3. The main determinants of peak latency under these conditions are therefore, spatial frequency and contrast.

Discussion

The implications of the results of these experiments are limited by the small number of subject studied, although the results are consistent with the data of Kulikowski (1977) and Arend (1976). [It should however be noted that the former did report that whilst the critical duration was independent of spatial frequency, there was some evidence of a more gradual decline in threshold beyond 'r' at the higher freqiencies.]. It would appear that, at the neural level, the critical duration (the interval over which contrast and duration can be manipulated to produce VEPs of approximately constant amplitude) is some 50-70 msec. If the high frequency gratings are detected only by 'sustained' channels then the results suggest that these mechanisms do not have a longer integration time constant.

An alternative explanation, is that there are no 'sustained' channels and the results can be explained in terms of band limited channels with differential response latency but constant integration time. Those who have advocated the existence of 'sustained' channels have supposed that because integration time constants of the postulated 'sustained' channels are approximately three to four times longer than the transient channels, it is ideally suited for the analysis of detailed visual information, and therefore is part of a form processing system. Crucial to this assumption is that the visual system needs 'time' to extract high spatial frequencies; at suprathreshold levels experimental data suggests that this is not in reality the case.

Significantly detailed visual information, to allow for the recognition of printed text, can be obtained within the first few milliseconds (50 msec) of stimulus presentation (Rayner et al,1981), and fixation times themselves last only 250-500 msec.

The increase in integration time constant for high spatial frequency gratings does not of itself imply the existence of specific 'channels' with long time constants. The relevant psychophysical data can be explained by other means. For example Rovamo & Virsu (1981) have shown that integration time is independent of spatial frequency when wave period is held constant, by varying viewing distance. This they suggest, implies that integration is not dependent on bar width but on the amount of spatial information to be integrated within the cortex. High frequency gratings, by this definition, have much more spatial information and will thus produce both a greater number and more complex patterns of neural events. Integration time does improve when the number of square cycles is increased and thus an increase in spatial detail leads to an increase in integration time constant.

The overall effect of spatial period will of course depend on field size and retinal location, because of the striate magnification factor (Cowey & Rolls,1964), but if this is compensated for, foveal and parafoveal integration times appear constant. (see Romanov & Virsu,1981). The data presented here does not directly support the conclusion of these workers, although the value of the integration time constant is similar, which may reflect the fact that their model is limited to interactions in the striate cortex alone.

Jeffreys (personal communication) had noted that the combined time course of the CI, CII and CII components is some 250-300 msec from stimulus onset, even for very brief pattern presentations. As these components are generated in retinotopically organised regions of cortex they reflect neural activity in a primarily 'sensory' system. The extraction of information from this neural activity could occur long after the offset of a contrast stimulus. Thus some of the increasing integration time constant at high spatial frequencies may reflect the increase in the extent and complexity of neural interactions within all regions of functionally distinct visual cortex for which the stimulus provides excitatory drive.

7.7:- Experiment 7.6:- Temporal resolution as a function of spatial frequency

The obvious corroborative experiment to that reported in the previous section would be to measure the temporal properties of CI as a function of spatial frequency/or element size for brief discrete pairs

of patterns as the interval between their onsets is progressively increased. It has been argued (Breitmeyer & Ganz,1976; Legge,1977) that gratings with spatial frequencies above 10 cpd are detected by 'sustained' channels, irrespective of temporal modulation rate. (Although see Kulikowski & Tolhurst (1973) who suggest that transient channels have high spatial cut off, see figure 7.2). At lower frequencies, detection would be determined by transient channels. Thus, if 'sustained' channels have, by definition, a longer integration time and a longer response time (see Coltheart,1980 and Breitmeyer,1979), then they might be predicted to have poorer temporal resolution. Indeed psychophysical evidence has been reported which supports this prediction, since it is observed that the thresholds for pattern detection (mediated by 'sustained' channels) is lower than for 'flicker' detection (mediated by 'transient' channels) (Green,1981).

Roufs (1974) has shown a relationship between the integration time constant for single time varying stimuli and for the limit of temporal summation for brief discrete pairs. However since the VEP data presented above have shown that the integration time constant is independent of spatial frequency, it can be predicted that the limit of temporal resolution should also remain invariant with regard to changes in the spatial content of the contrast pattern.

Procedure

The general procedure was similar to that used in the chapter 4. Briefly, three fields of the tachistoscope were used, one of which contained the contrast pattern positioned in the left or right half field. This field was switched twice during the aperiodic cycle. The third field was continuously illuminated and thus allowed the modification of stimulus contrast whilst keeping overall mean luminance constant. The experiments were undertaken on two subjects, for one an extensive range of pattern element sizes were examined, whilst for the other only the two extreme (highest and lowest) spatial frequencies were used.

In part one, square wave gratings ranging in frequency from 1-10 cpd were presented. At higher spatial frequencies the VEP becomes small even at high contrast. Thus to allow the exploration of this range, for which only sustained channels would be expected to be operative, isolated outline square patterns of constant square size (16 arc) but of differing line width were used. The paradigm used here was to present such stimuli with a constant square size and inter-square

separation but of varying line width. It is thus possible to record VEPs to squares, the line width of which are eqivalent to the bar width of a 50 cpd square wave grating (some 0.6°arc).

It may be argued that although the line width of these stimuli has varied, their fundamental Fourier components have not. It is not known where these components lie, although is is obvious that the energy distribution will be a function of line width. Each stimulus was presented at a contrast of 0.20 and had a presentation time twice the psychophysically determined duration threshold.

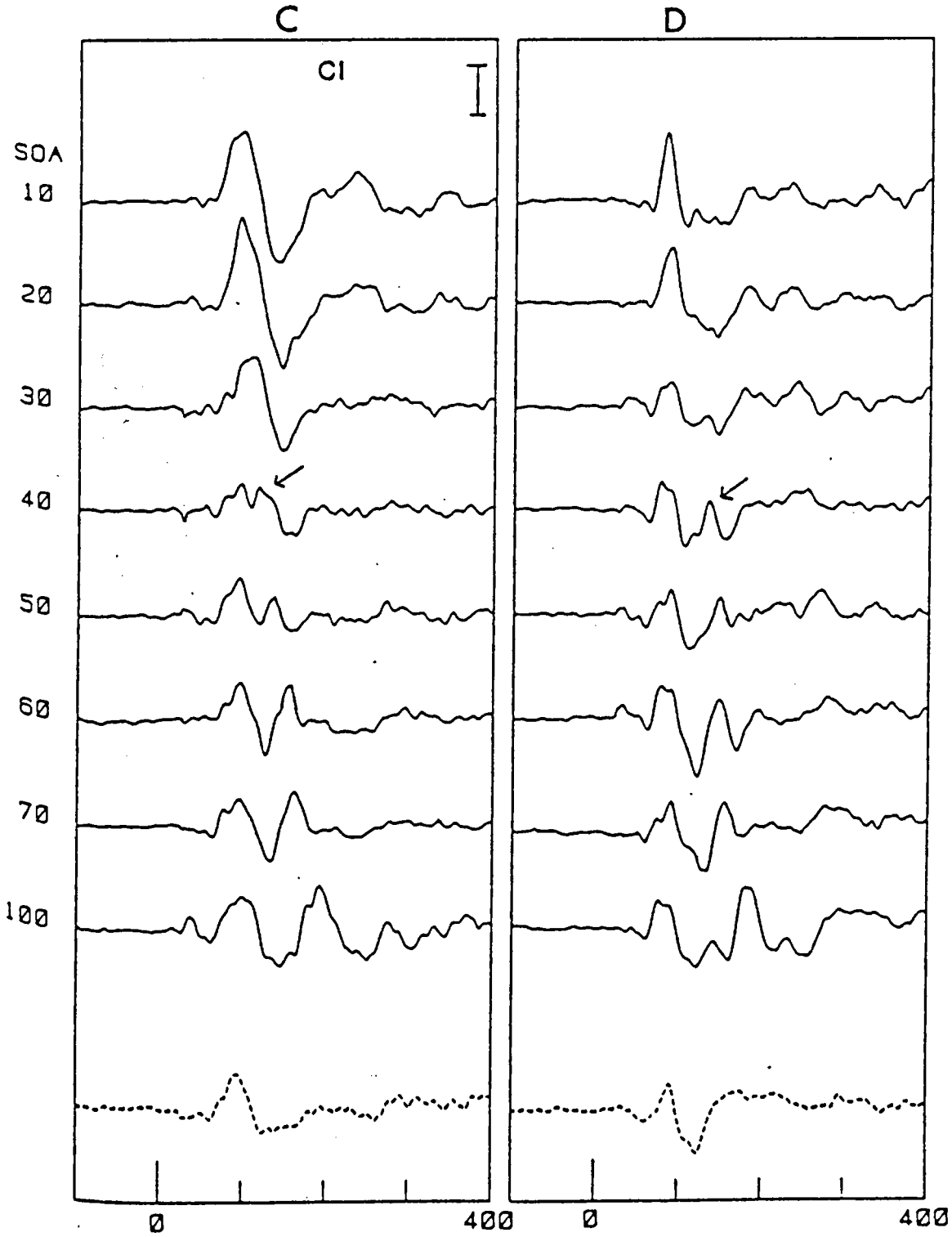
Results & Discussion

The results of these experiments have been shown in figures 7.12a-b for subject H.D and in figures 7.13a-d for subject M.J.M. Rather than attempting to quantify limiting resolution for each stimulus pair and plotting the results graphically, the actual waveforms have been shown because they give a clearer idea of the time course of the VEPs elicited by brief sequential pairs.

The limit of resolution, defined as in chapter 4 is indicated by an arrow above the appropriate peak in each figure. It is evident that the limit of resolution for this component of the VEP is independent of spatial frequency for both square wave gratings between 1-10 cpd and isolated square outlines with line widths down to 0.6°arc. There is some evidence that at lower spatial frequencies (below 3.5 cpd) the limiting resolution drops below 50-60 msec to a value of 40 msec, if this effect is the result of transient channel stimulation then it can be stated that limiting resolution for this system is some 20 msec lower than that for the high spatial frequency detecting mechanism (sustained channel). Even so this difference is several orders of magnitude lower than that which would be predicted from the psychophysical data of Legge (1977) and Breitmeyer & Ganz (1977).

The time course of temporal summation for a range of stimulus types has been plotted in figures 7.14.

It is possible that the field size used in this study has led to these unexpectedly low limits of temporal resolution at high frequencies, because it selectively favours the stimulation of transient channels over sustained ones, the latter being limited to the foveal region (Ikeda & Wright,1972; see also chapter 1). Two points can be made to question this suggestion.


C
D
CI
SOA
10
20
30
40
50
60
70
100
0
400
0
400

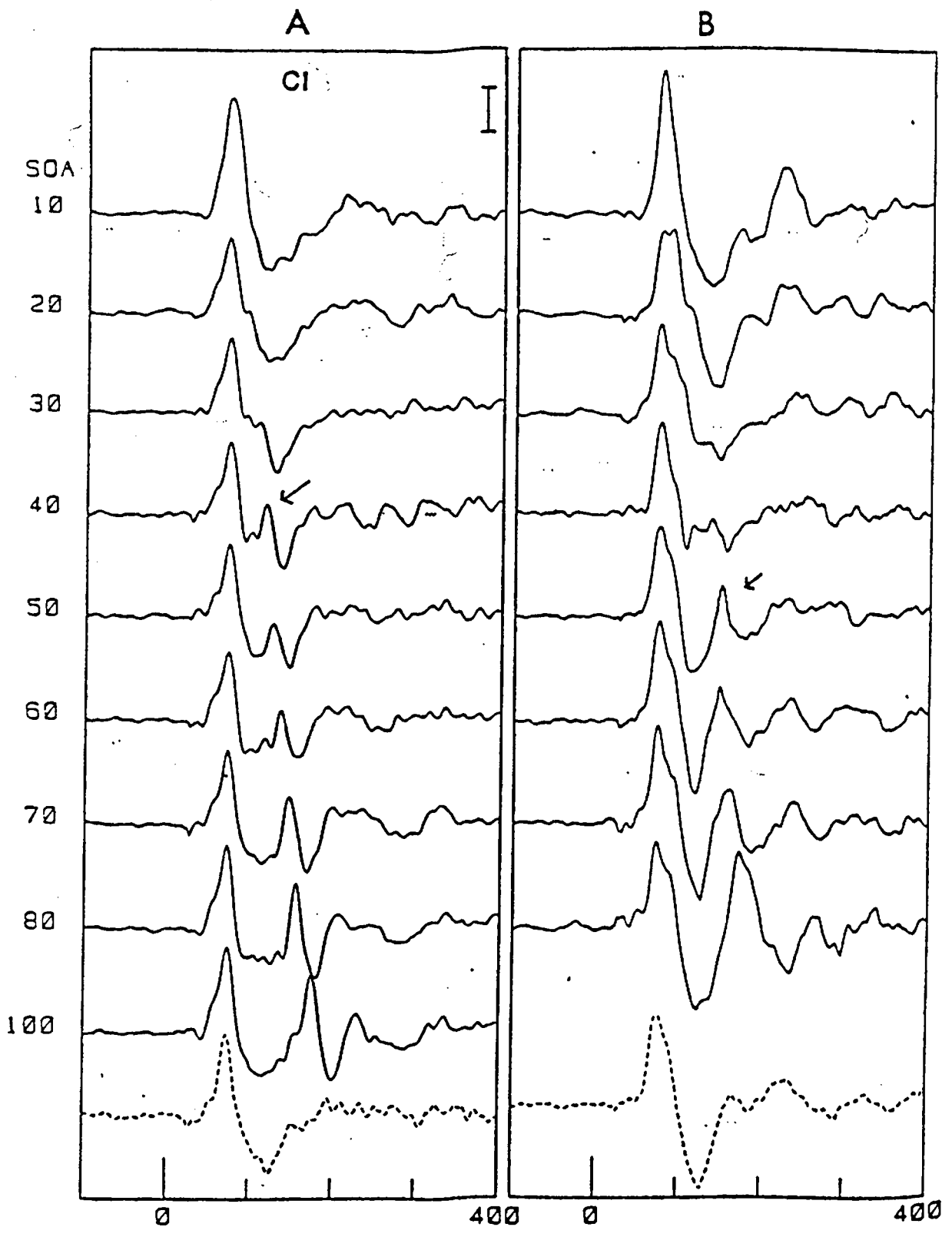


Figure 7-12a-b

CI for subject H.D. elicited by pairs of near threshold grating and isolated square outline patterns.

Column A:- Isolated squares 4.6'arc line width.

B:- Square wave grating, 1.5 cycles/degree.

C:- Square wave grating, 10 cycles/degree.

D:- Isolated squares 0.6' arc line width.

Dashed waveforms are elicited by a single prsentation.

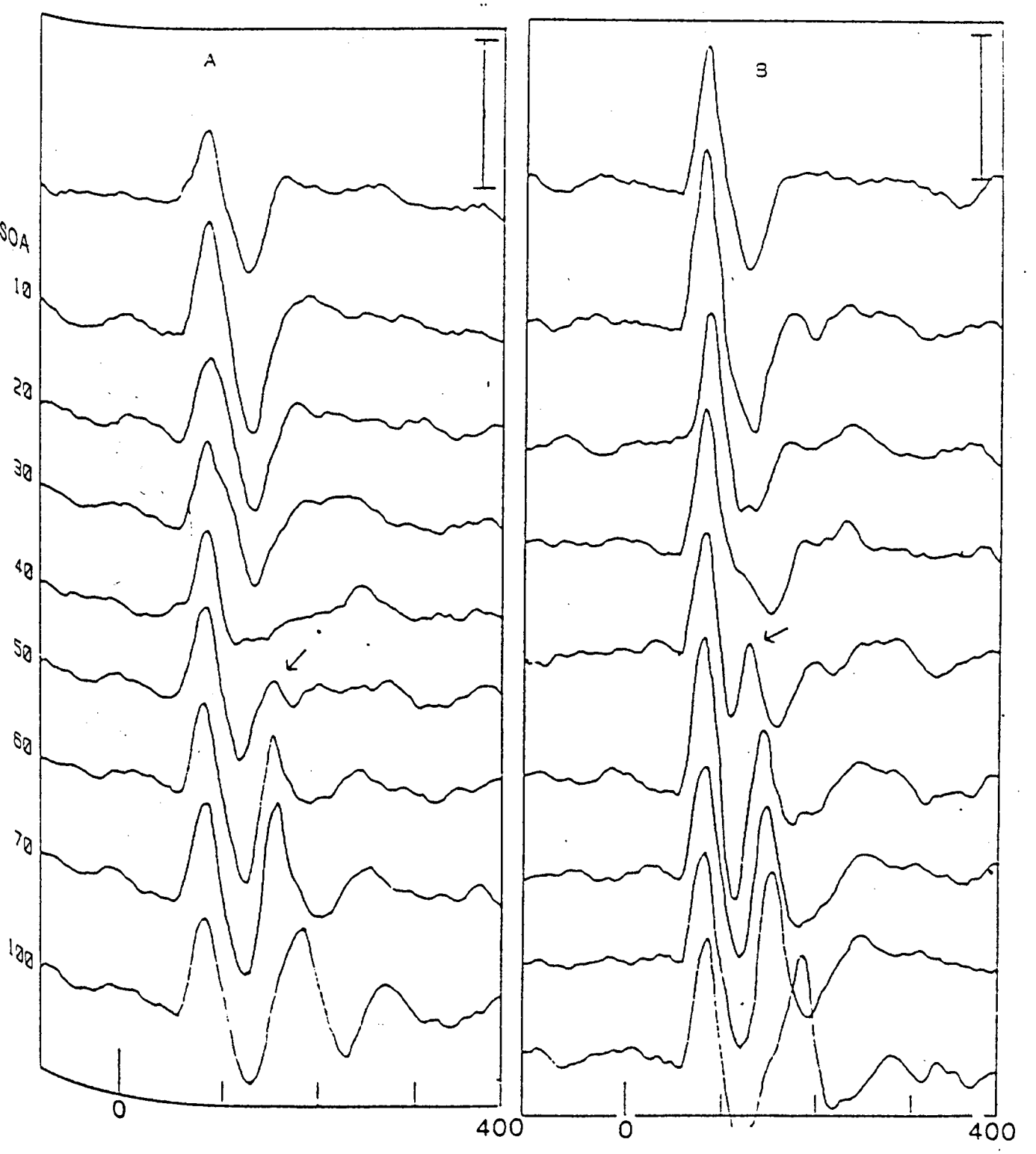
Figure 7.13a-d

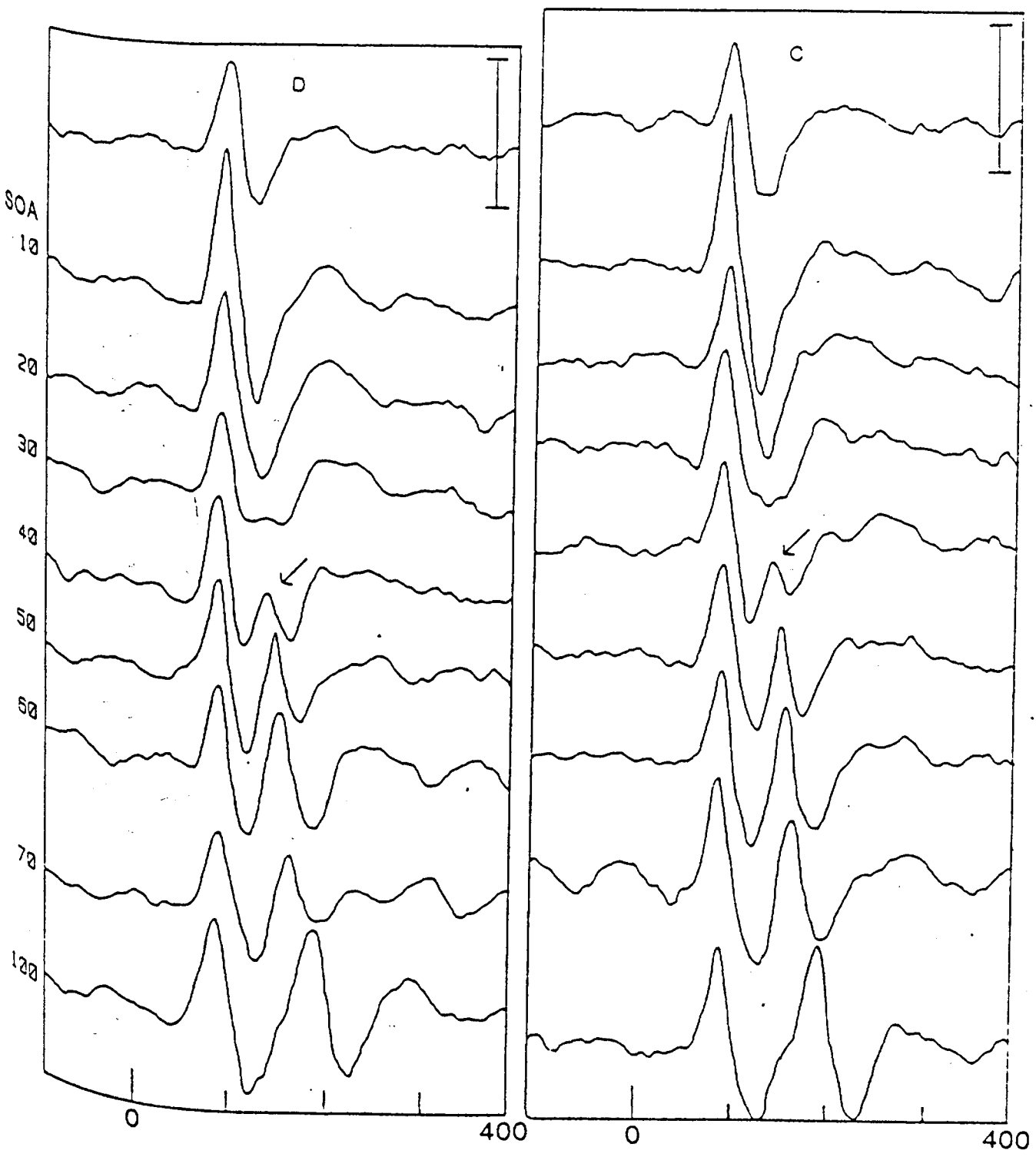
VEPs recorded from subject M.J.M. to brief pairs of grating or isolated square outline stimuli. Stimulus contrast was 0.20 and each stimulus was presented at twice their respective duration thresholds.

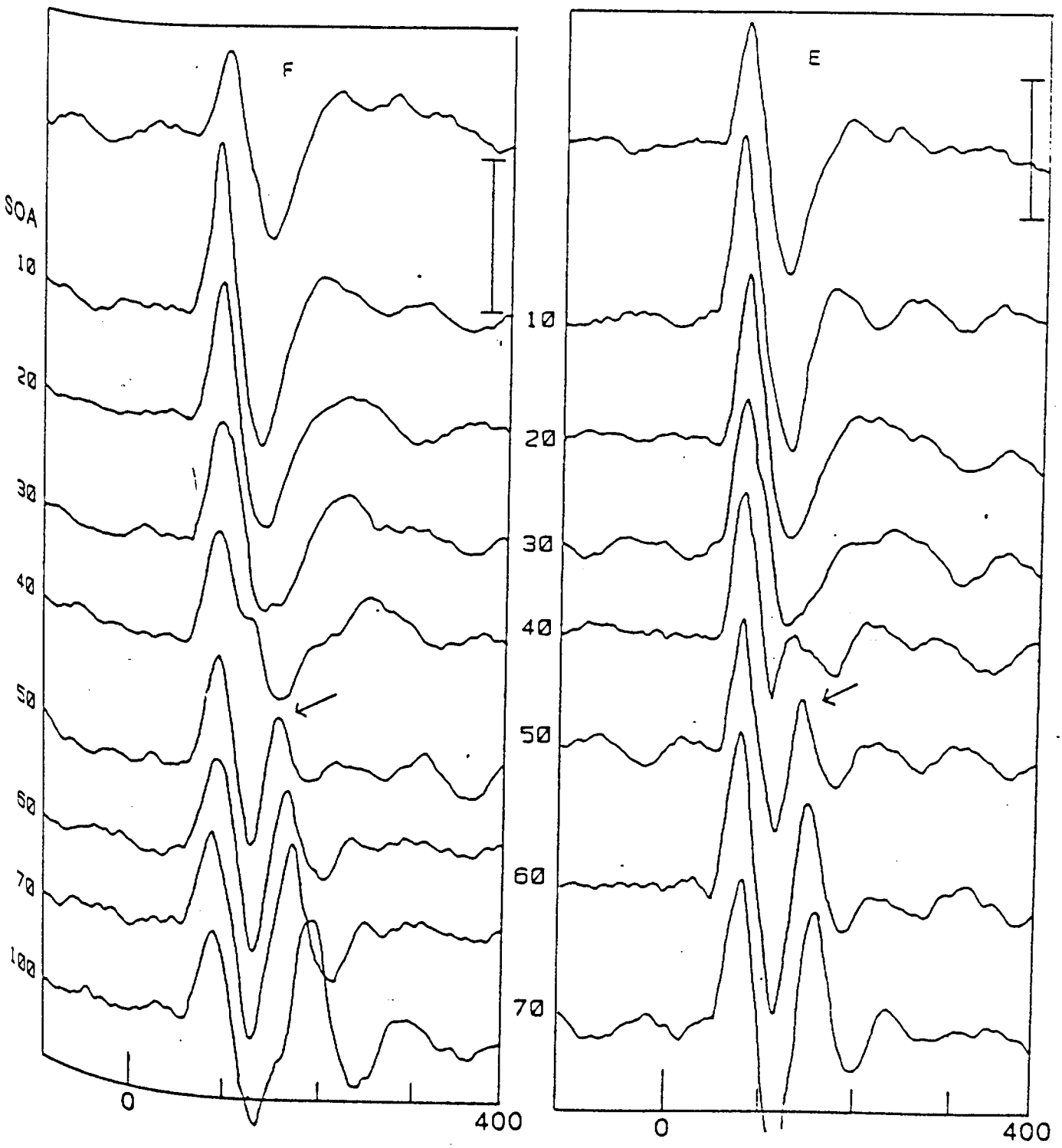
Column A:- 0.75 cpd square wave
B:- 3.5 cpd
C:- 7.5 cpd
D:- 10.0 cpd
E:- 5.4 cpd

Isolated square patterns.

Column F:- 1.8 min arc line width
G:- 1.2 min arc line width
H:- 0.6 min arc line width (contrast 1.00). See text for more detailed discussion.


A
B
SOA
10
20
30
40
50
60
70
100
0
400
0
400


D
C
SOA
10
20
30
40
50
60
70
100
0
400
0
400


F
E
SOA
10
20
30
40
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100
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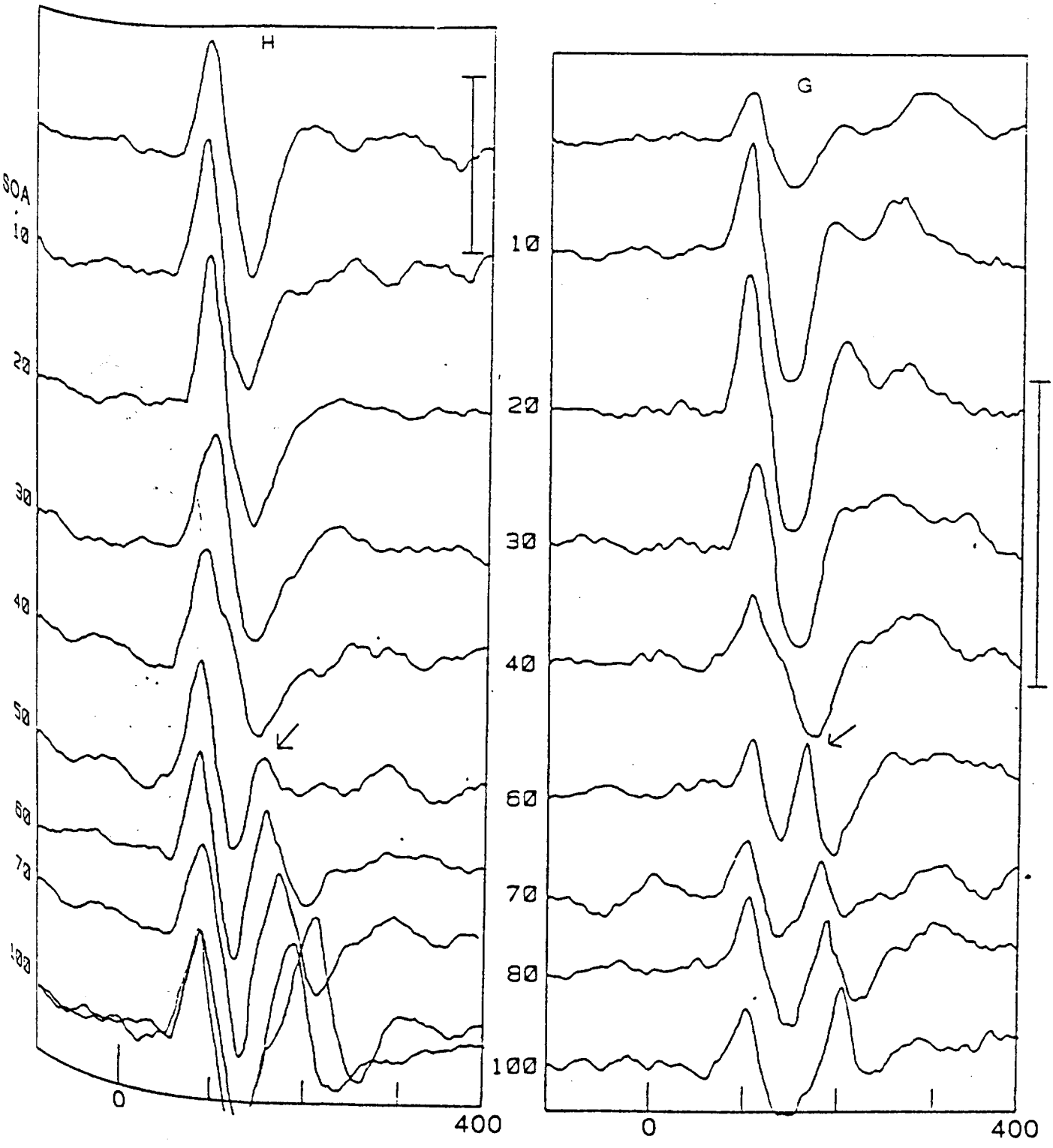
H
G
SOA
10
20
30
40
50
60
70
80
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0
400
0
400

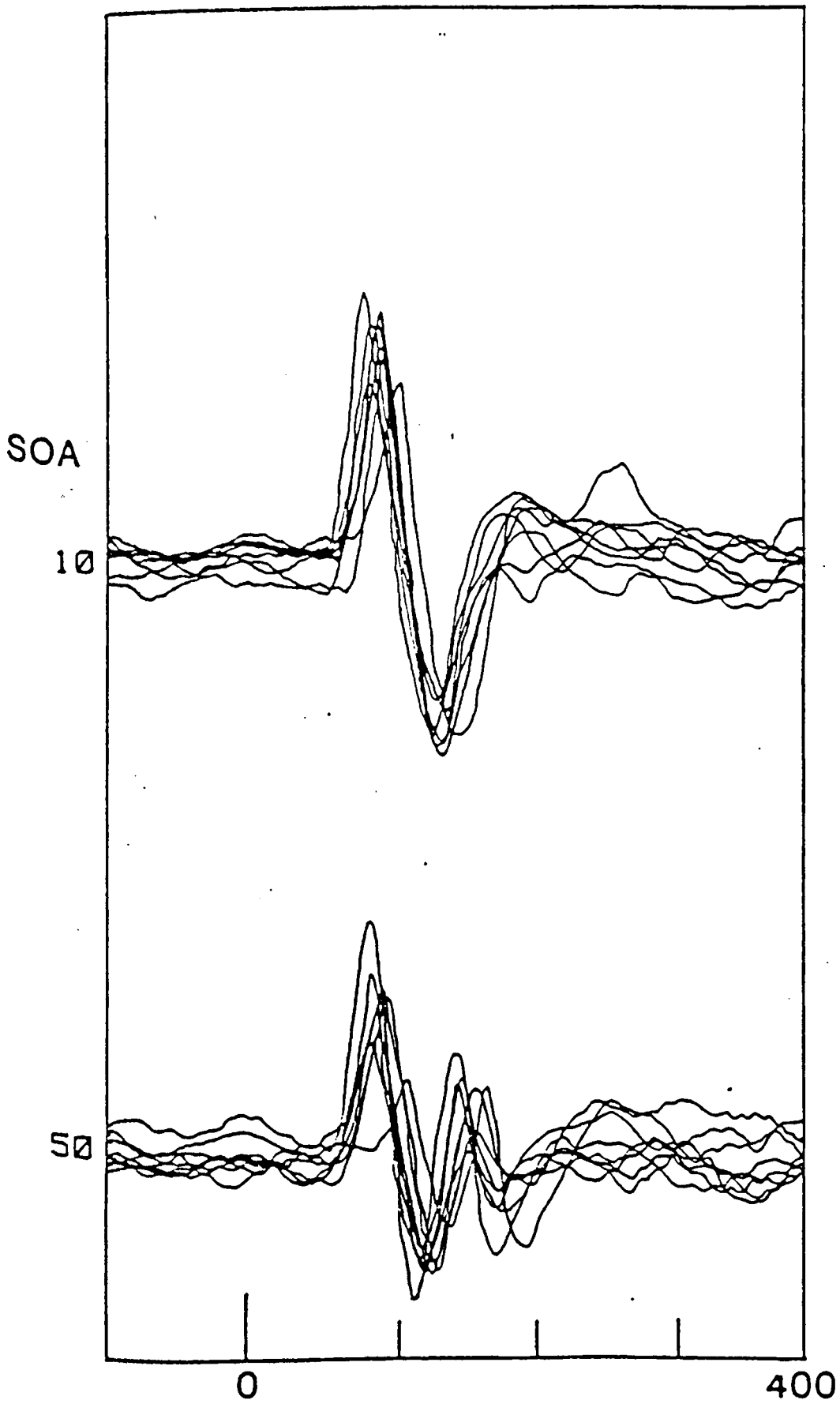


Figure 7.13e

Superimposed waveforms for each of the 8 stimulus conditions for subject M.J.M. at 10 and 50 msec SOA. This figure illustrates that the effect of reducing stimulus width from 45'arc to 0.6'arc is to increase the peak latency of CI by some 30 msec, but leaves the limit of resolution unchanged.

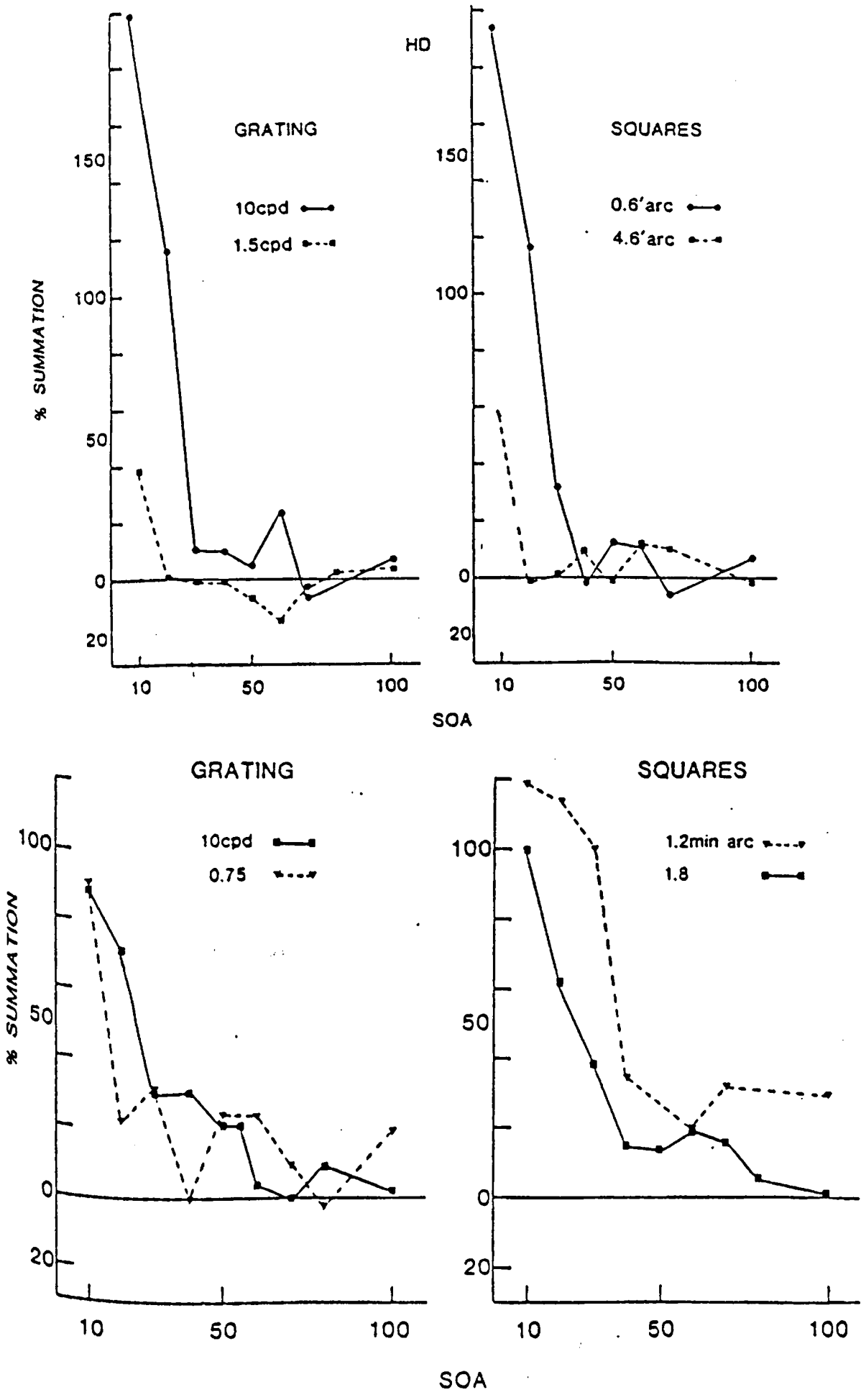


Figure 7.14

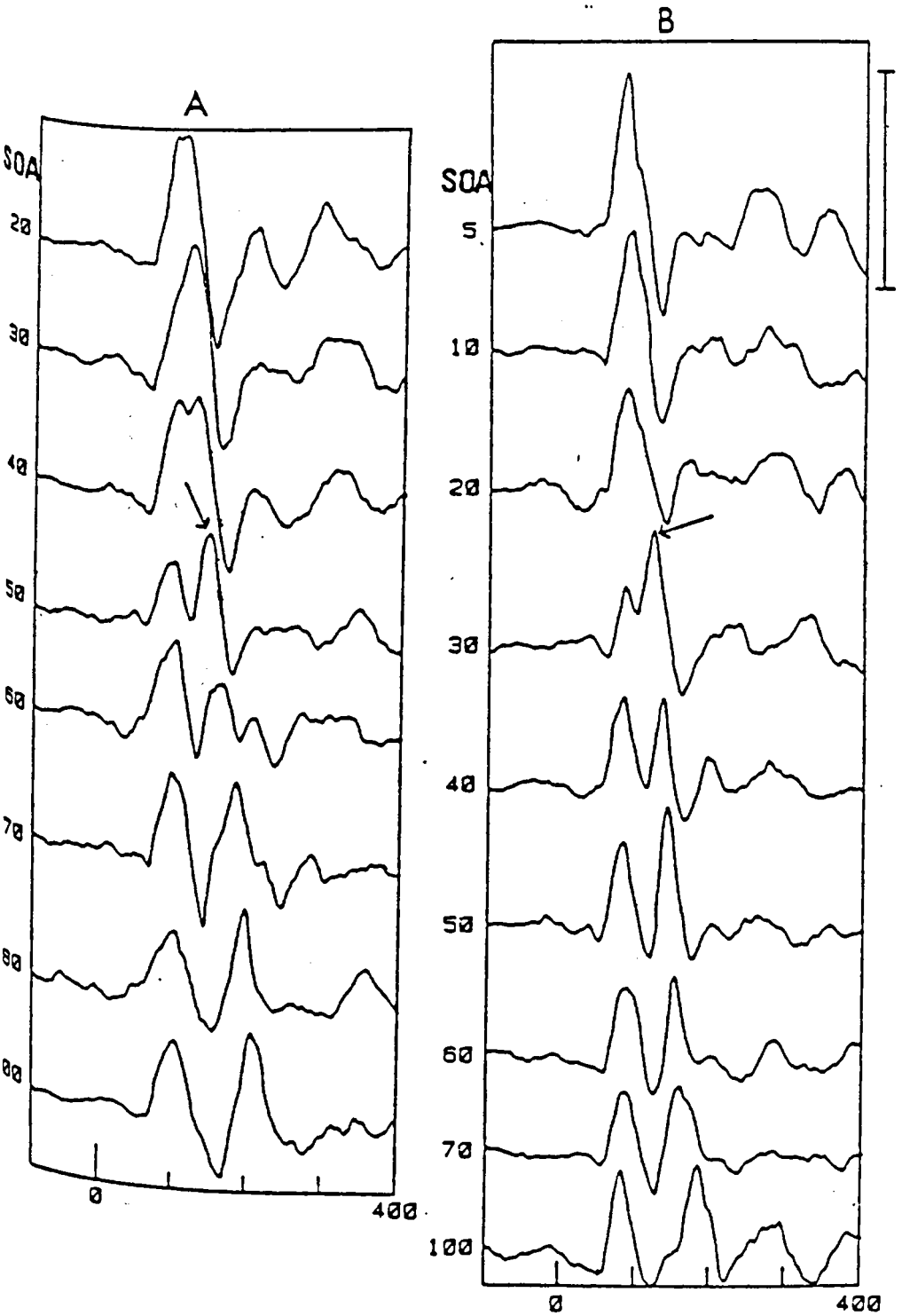
Illustrates for two subjects the time course of component summation for gratings and outline squares of variable line width as a function of SOA. The time course of summation is similar in each case, being complete only at short SOAs.

Firstly, duration thresholds were defined as the minimum duration for which any temporal modulation within the field could be detected, and this point, particularly for the isolated squares of small line width was confined to the central 1 to 1.5 degrees. Contrast thresholds are not constant as a function of retinal location (Anstis,1974) and thus even when the duration of the stimulus was increased to twice threshold duration much of the peripheral regions of the stimulus remained undetected.

Secondly, the patterns used had been chosen precisely because they would be detected only by a high acuity, i.e., a foveal mechanism. The properties of sustained and transient channels have been characterised such that three of the stimuli used in this study would, by most estimates of their acuity, be well outside the spatial range over which the latter would be expected to respond (Breitmeyer & Ganz,1976). It should be noted that the latency difference between VEP elicited by the finest line width of isolated square and the coarsest grating was some 30 msec, (see figure 7.13e).

As a final control the above experiment was repeated on one subject with different types of patterns, each of which was presented at twice the threshold duration and at a contrast of 0.20. The stimuli are shown in figure 7.15 along with the evoked response. The radially expanding square wave grating was chosen to optimally stimulate postulated transient channels. The random vertical and horizontal line elements were chosen to optimally stimulate postulated sustained channels. The length of each line segment was 24°arc in length with a width of 1.2°arc. The duration of the radially expanding grating was 2 msec that of the random line segments 12 msec.

The waveforms presented in figures 7.15 indicate that the limit of resolution for the grating was 30 msec, that for the random line segments 50 msec SOA. It is interesting to note that a latency difference of 20 msec is also observed between the postulated contour and contrast components of CI (see chapter 13). In the present experiments it would be predicted that the line segments would optimally stimulate the contour specific mechanims of striate cortex, whilst the grating would be predicted to stimulate mainly contrast specific processes.



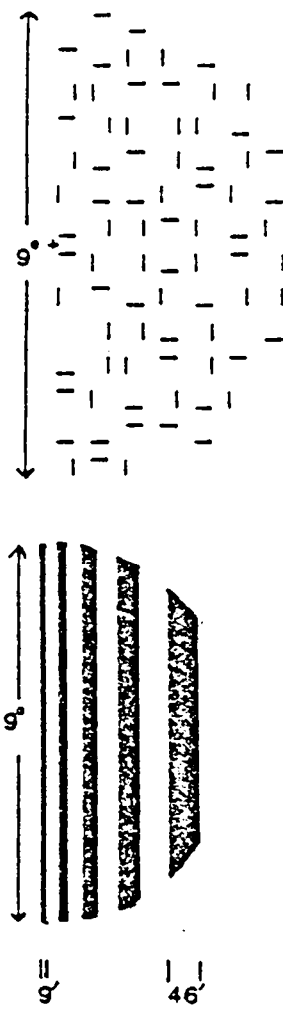


Figure 7.15

Illustrates stimuli chosen to optimally stimulate so called 'sustained' (line elements) and 'transient' (grating) channels. The VEPs elicited by line elements (12'arc long and 1'arc wide) are shown in column A, and the gratings in column B.

of Schiller & Malpelli (1977) and Dreher (1976) suggests that impulses from the fast group (so-called Broad Band cells) have a retino-cortical latency of 6 msec,those of the opponent group a latency of 10 - 15 msec. It is thus unrealistic to suggest that the postulated latency difference of some 100-150 msec between the sustained and transient channels correlates with that observed between 'X' and 'Y' type cells as suggested by Breitmeyer & Ganz (1976).

Much of the reported psychophysical data on this aspect of visual processing has been explained in terms of the properties of cell types recorded from the cat. Whilst 'X' like and 'Y' like cells, (the so-called phasic and tonic class), have been reported in monkey, recent studies suggest that there are substantial differences not only in specific properties but in the sites to which they project (see chapter 1).

Although there appears to be a distinct dichotomy between cells populations within the parvocellular layers (PCL) and magnocellular layers (MCL), of the LGN, this dichotomy is not consistent with a simple 'sustained/transient' distinction, (see Lee & Cleland,1980).

Lennie (1980) has noted however that the extent to which cells have a sustained or transient response is dependent on adaptation level, the more light-adapted a cell, the more transient its discharge, irrespective of its type (Enroth-Cugell & Shapley,1973). Light adaptation is dependent on photon capture, the amount of which will be determined, for each cell, by receptive field size and, since 'Y' cells have on the whole larger receptive fields and hence capture more photons at low adaptation levels, they will thus have a more transient response. Also, the time course of response to contrast stimuli will depend on their suprathreshold level; there is little difference in the time course of the response of 'X' and 'Y' cells near threshold contrast levels (Lennie,1980).

Visual acuity (related to receptive field size) of 'Y' cells in cat is reported to be poorer than that of the 'X' type, although the extent of this difference will be dependent on receptive field position; foveal 'Y' cells are reported to have similar acuity to 'X' cells (Lennie,1980). The PCL and MCL cells in monkey have similar acuity (Lee & Cleland,1980).

Hicks, Lee & Vidyasagar (1981) note that the major difference between PCL and MCL cells was the slightly lower spatial tuning of the latter, which is direct evidence that the 'X'-like cells in monkey are

The results show that those neural mechanism processing high spatial frequencies have very similar temporal properties to those processing very low frequencies.

7.8:- General Discussion. Part II

The results of this series of experiments suggest that much of the speculation regarding the locus and neurophysiological correlates of the sustained/transient channel theory of visual information processing is wrong, (see also (Lennie,1981).

Only two types of psychophysical data appear consistent with the properties of 'X' and 'Y' cells. Specifically, the finding that the MTF for fine spatial gratings is lower than that for coarse ones, which is consistent with the finding that 'Y' cells respond to gratings drifted across the receptive field at high temporal frequencies, whilst 'X' cells do not; and that 'X' cells have small receptive field and 'Y' cells do not. Even here the results are not clear cut; Lennie (1979) has shown, for example, that when cat 'Y' cells are tested under conditions commonly purported to reveal the existence of two types of processing channels in man, they are no less sensitive than 'X' cells to threshold stimuli of low temporal modulation rate.

The major factor thought to be consistent with the single unit data has been the increase in RT latency as a function of spatial frequency. The large latency differences differences thought to characterise these two channels then form the basis for the postulated temporally dependent interactions between them; as in the phenomena of metacontrast and visual noise masking (see chapter 8 and 9, see also Breitmeyer,1981). Yet single unit data has never shown large latency differences between 'X' and 'Y' cells. For example, Ikeda & Wright (1975), reported response latencies for cortical sustained and transient cells which showed considerable overlap, with a mean latency for sustained cells of 57.2 msec and for transient cells of 46.7 msec, whilst the overall difference in conduction velocity from retina to cortex, was for the former 7 - 14.2 msec and the latter 4.4 - 6.4 msec, the bulk of the increase in the latency of cortical response being determined by interactions within the retina.

In monkey, where the optic tract fibers have slower conduction velocities, the overall latency will be increased. However whilst there are no comparable data for monkey to that of Ikeda's for cat, the work

not homologous with the sustained channels reported in man, or indeed identified psychophysically in the same species of monkey as reported by Harwerth, Levi & Boltz (1977).

Thus, many of the assumptions which have been made regarding the neuronal substrates of the sustained/transient model postulated for man, are not consistent with the relevant single unit data in either cat or monkey (see Lennie, 1980). The VEP data reported in this chapter provided electrophysiological evidence that the neuronal basis of these channels are unlikely to be within the retino striate pathways.

Chapter 8:- VEP studies of metacontrast phenomena

Introduction

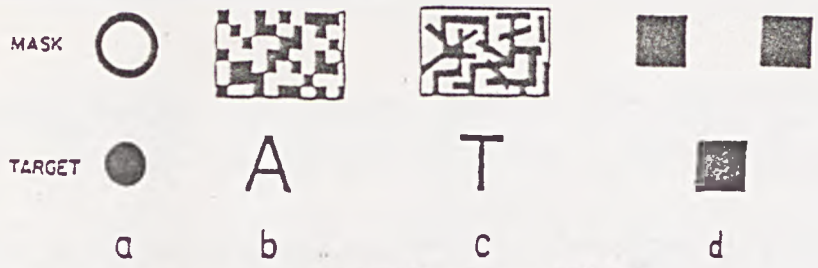
Any general theory of visual perception will have to account for the phenomena of visual pattern masking, of which there would seem to be three types (see Kahneman,1968; Weisstein,1972; for a recent review see Breitmeyer & Ganz,1976). In figure 8.1.2 are shown the typical masking functions obtained under the three types of conditions. According to the nomenclature of Kohlers (1962) figure 8.1.2(a) represents the type 'A' effect, whereby masking magnitude is maximal at the simultaneous presentation of the target and its masker, and decreases monotonically as the absolute value of the SOA increases, as is illustrated by the data from Sperling (1965) in figure 8.1.3

Figure 8.1.2(b) shows the type 'B' masking function, where masking is maximal for non-zero SOAs and is described by an inverted 'U' shaped function which for negative SOAs (mask precedes target) is called paracontrast and for positive SOAs (target precedes mask) is termed metacontrast. The figure from Alpern (1953) (figure 8.1.4) illustrates typical experimental data.

The masking functions obtained in any particular experimental condition will depend critically upon such factors as the spatial configuration of the target and mask, their retinal locations and their energy or intensity ratios (see Weisstein (1973) for details). In general, type 'A' effects are obtained when the masking stimulus is both spatially contiguous with and of greater subjective or physical intensity than the target (Kinsbourne & Warrington 1962). A more detailed account of these masking phenomena will be given in chapter 9. Stimuli (b) and (c) in figure 8.1.1 will produce type 'A' effects.

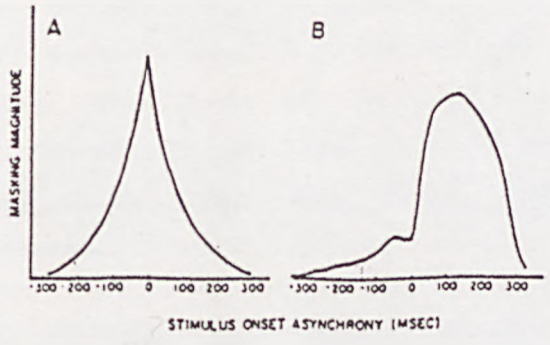
Type 'B' masking functions are obtained with spatially non-contiguous target/mask configurations ((a) and (d) in figure 8.1.1). Masking is maximal when both stimuli are similar in form, and decreases markedly for stimuli that are of a different category, i.e., a small square will not be masked by the presentation of two similar sized circles which flank it on either side, although when the circles are replaced by squares similar in size to the target masking will be observed. Indeed Uttal (1970) has shown that the extent to which

1



Mask and target stimuli typically used in (a) metacontrast and paracontrast masking, (b) masking by noise, and (c) masking by structure.

2



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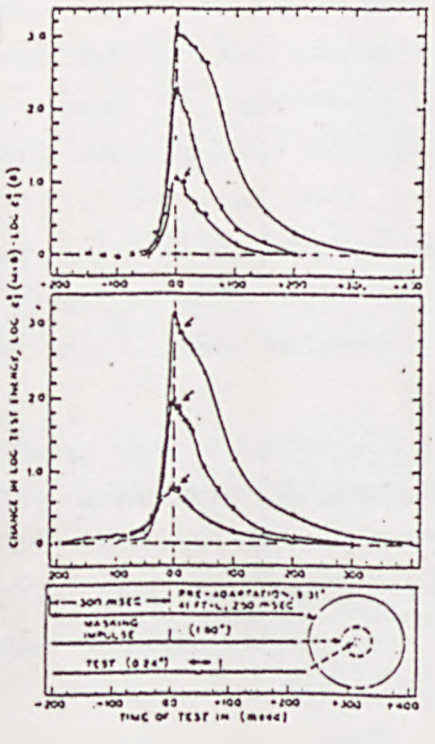
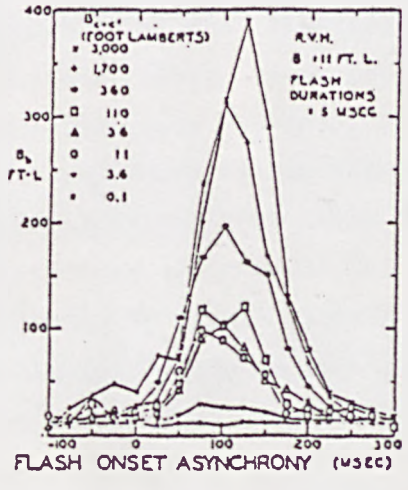


Masking by homogeneous light. After preadaptation a smaller masking disk and an even smaller concentric probe spot (both very brief) are presented at some SOA value. The results depict the log threshold energy for the detection of the spot as a function of SOA.

[From Sperling (1965).]

4



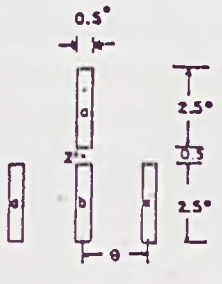


Figure 8.1

Typical masking fuctions obtained under metacontrast and noise masking conditions.

For metacontrast (fig 2.A) maximal masking occurs at some 100 msec after target stimulus onset.

This type of phenomena is further illustated in figure 4 which is taken from Alpern (1953). The masking stimuli are shown below as bars marked 'a'. The target is bar 'b', and the upper bar marked 'a' is a comparison stimulus against which the contrast of bar 'b' is compared. Under these conditions the form of the masking function shows maximal masking at around 100 msec SOA for stimuli that are 5 msec duration.

The monotonic masking function produced by spatial and partially spatially contiguous stimuli shown as 'b' and 'c' in figure 8.1.2(b) is illustrated by experimental data taken from Sperling (1965).

metacontrast masking will occur depends very critically on the similarity in form of target and mask.

The aim of the experiments reported in this chapter is to examine the properties of the CI and CII components under stimulus conditions that give rise to metacontrast, and thereby to test the predictions of two models of the phenomenon which will be briefly outlined below. The experiments are divided into two main parts. Firstly, multi-element targets and masks will be used to elicit the CI component. Such stimuli are not commonly used in psychophysical studies, but have the advantage that they give rise to large and repeatable VEPs, the properties of which are easily quantified. A short psychophysical study will also be reported which shows that these novel types of stimuli give rise to metacontrast.

The stimuli were variations of the configurations shown in (a) and (d) of figure 8.1.1. In experiment 8.1 the flanking squares paradigm will be used. This configuration gives rise not only to metacontrast but also produces apparent motion (see Kahneman,1967). For this reason in experiments 8.2 and 8.3 two forms of the disc-annulus masking were studied to extend the implications that could be drawn from this VEP data with regard explanations of metacontrast. In the second part of the chapter the VEPs elicited by single element targets and flanking masks will be recorded. These conditions will replicate those under which metacontrast has been studied psychophysically.

There are a number of physical constraints on the properties of stimuli which can be shown to produce metacontrast, for example both target and mask must be similar in intensity or energy. Increasing the relative mask to target intensity ratio produces a more monotonic masking function (Breitmeyer & Ganz,1976). It has also been suggested that target and masker must be similar in chromaticity (Breitmeyer & Ganz,1976), although there is now evidence that metacontrast can be observed between isoluminant opponent colour stimuli (Reeves,1981; see also discussion).

It is not only the form of the target and its masker that can be shown to influence the masking function, response measures have also been reported to differentially influence its extent (Raab,1964). The classical metacontrast effect is a reduction in the subjective contrast or intensity of the target, dependent on the successive presentation of a flanking mask; thus measures such as brightness ratings, contour

discrimination, and magnitude estimation (Weisstein,1969) have all been shown to produce a typically non-monotonic masking function. However such a function is not found if a forced choice detection, or reaction time paradigm is used (Feher & Raab,1962; Schiller & Smith,1966). Two points need to be made however. The first is that as the metacontrast phenomenon is essentially a reduction in the subjective contrast of the target it is unlikely that a detection criteria or reaction time measure would show up this effect, simply because they are not very sensitive measurements of sensation.

Secondly, whilst some stimulus configurations produce a considerable reduction in the subjective contrast of the target, they do not necessarily make the target completely invisible; this is particularly true for stimuli with a large angular subtense, similar to those used by Schiller & Smith (1966). Complete erasure of the target can be achieved by the use of relatively small stimuli, 5-10'arc, thus refuting the suggestion (Erikson et al,1970) that metacontrast phenomena are merely a 'figment' of response criteria.

8.1:- Models of metacontrast phenomena

A number of models have been introduced to account for the large body of experimental data that now exist relating to metacontrast phenomena, these models can be divided into two main classes. On the one hand are those of Uttal (1970) and Turvey (1972) which have stressed the importance of what may be loosely described as "cognitive" factors and which explain the observed interactions in terms of concepts which owe much to infomation theory. The predictions of such models are not directly open to electrophysiological investigation, since they do not make specific claims as to the types and site of the neural interactions underlying these "cognitive" phenomena.

The second class of model, such as proposed by Weisstein (1969; 1972) Breitmeyer & Ganz (1976) and Bridgeman (1972), are physiologically orientated and are based on known or postulated functional physiology of the visual system (much of it derived from studies of the cat).

Briefly, Weisstein's (1973) model is based on a modified Rashevsky-Landel neuronal net comprised of five two factor neurons with the added assumption that, "under some conditions", inhibition can develop at the cortical level some '50-100 msec' earlier than

Figure 8.2

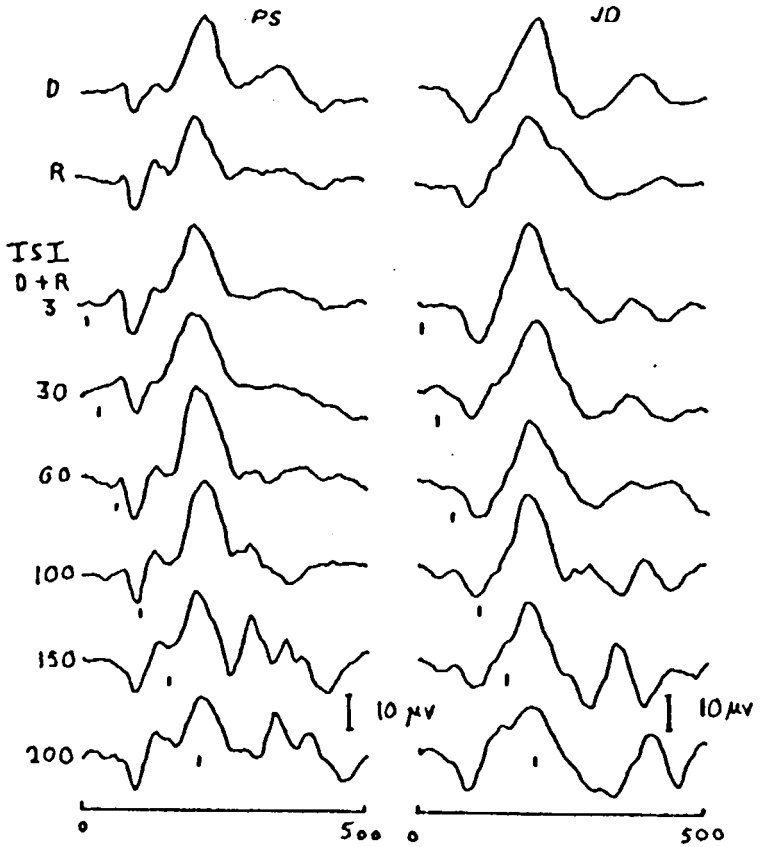
Illustrates the models of Breitmeyer & Ganz (1976) and of Weisstein (1973).

The Breitmeyer & Ganz model (left of page) assumes that visual system is composed of two distinct channels with different spatial and temporal tuning, as illustrated in the bottom right and upper left figures.

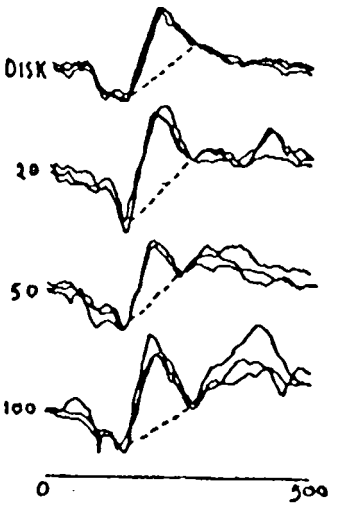
The latency of response at cortex will depend on the spatial content a stimulus, and as the figure suggest this model assumes that there is a 100 msec plus range of latency difference between high and low frequencies. Thus for high spatial frequency targets the time course of maximal masking will be longer than that of low fequency targets.

The assumed interactions between sustained and transient channels are mediated by interneurons at the LGN and cortex, (middle figure left) which also showns the implied time course of sustained (target) and transient (mask) activated responses.(see text for further discussion).

The model of Weisstein is illustrated in the top right figure. The overall predictions of this model are the same as that of the former, but in this case the assumption is that activity in the target neuron is inhibited by fast acting inhibition mediated by interneurons stimulated by the subsequent mask.



Schiller '66.



Vaughan et al 68.

Figure 8.3

VEP data from Vaughan et al and Schiller & Chorover (1966) commonly reported to show evidence for and against, VEP correlates of metacontrast interactions, respectively.

The 'hump' in Vaughan's VEPs above the dashed line has been measured. Because this 'hump' at 50 msec ISI is smaller than that observed at 20 or 100 msec, and because at this ISI subjects report target dimming it was concluded that this was evidence of a cortical locus of the phenomena.

Shiller concluded the opposite from his data. He measured the small negative peak in the initial phase of the waveform although no reason why this was done.

Figure 8.3b

From Andressi et al (1976). The three conditions denoted by the Roman numerals represent three different stimulus conditions, in which, for condition I, all three stimuli (denoted by numbers 1,2 and 3) were the same or in II only 1 and 2 were the same or III were each stimulus, 1,2 and 3 differed. The conclusion of this study was that when all three stimuli were the same (I) the 'subjective metacontrast' observed in sub-condition B and C correlated with a decrease in the amplitude of the resulting VEP. Similarly in B of (II) the decrease in the amplitude of the VEP to the target (stimulus 1) was consistent with the reduction in subjective contrast of the latter, whilst in experiment III where all three stimuli differed and thus no decrease in subjective contrast was observed the VEP elicited in condition B and C correlated with this. The differences in VEP amplitude were reported to be statistically significant.

excitation (see figure 8.2). The crucial assumption of the model is that metacontrast does indeed have a cortical locus, and its interocular transfer (Schiller & Smith,1968) and the importance of target/mask spatial configuration and separation are taken as supportive evidence.

Evidence consistent with this suggestion comes also from VEP studies of metacontrast, and Weisstein has cited the data of Donchin & Lindsey (1965) and Vaughan & Silverstein (1969) (see figure 8.3(a).) to support the notion that neural activity evoked by the target is inhibited by the mask because the VEP elicited by the former appears, in these studies, to have been attenuated. However such studies, along with that of Andreassi et al(1976) (see figure 8.3(b)), are of limited importance since no attempt has been made to study isolated VEP components.

Breitmeyer & Ganz's (1976) explanation of metacontrast (see figure 8.2 for diagrammatic description) relies upon evidence of functional differences between the 'X' and 'Y' type cells reported in the cat (see chapter 1) There are two main assumptions underlying the model which are:-

A:- that 'sustained' channels are vital for the processing of 'form' information, and that these channels can under certain conditions be inhibited by 'transient' channels.

B:- that the latency of response of the 'sustained' channels is some 70-100 msec longer than that of the transient channels.

Some of the psychophysical evidence supporting assumption B has been reviewed in chapter 7. The evidence of transient inhibition of sustained channels comes form a single study showing that the Y type cells inhibit X type cells at the level of the lateral geniculate body of the cat (Singer & Bedworth,1973).

In spite of the very tenuous physiological basis for the 'sustained-transient' model, it has received much support. However, the limitations of previously reported VEP studies cited as corroborative electrophysiological evidence, necessitates a more detailed study, in which the properties of isolated VEP components of predicted source locus are examined in a metacontrast paradigm.

The following has been redacted from this digital copy of the original thesis at the request of the awarding university:

Fig. 1.4a between pages 11 & 12

Fig. 3.11 between pages 29 & 30

Fig. 3.12 between pages 31 & 32

Fig. 3.13 between pages 31 & 32

Fig. 4.8 between pages 48 & 49

Fig. 5.1 between pages 52 & 53

Fig. 7.1 between pages 80 & 81

Fig. 8.2 between pages 101 & 102

Fig. 8.3b between pages 101 & 102

Fig. 8.12 between pages 110 & 111

Fig. 8.13 between pages 112 & 113

8.2:- Part 1 - Flanking target/mask metacontrast

Procedure

The stimuli were a modified version of those used by Kahneman (1967). The target pattern consisted of three rows of 16'arc squares with a spatial separation of 6'arc. The mask pattern comprised of four rows of isolated squares of equivalent size to that of the target. There was a 6'arc separation between the target squares and the squares of the flanking mask. Both stimuli in the present experiment had a physical contrast of 1.00 and had a fixed duration of 10 msec. The stimuli were well above their respective thresholds.

For one subject (M.J.M.), VEPs were also recorded when the target and mask were presented as positive contrast stimuli on a background of 400 cdm^{-2}. Stimulus duration was again set at 10 msec and the luminance of the squares adjusted so that they had an equivalent threshold duration to that of the negative contrast patterns.

To assess the extent and form of the subjective metacontrast produced by these stimuli, a Magnitude Estimation experiment was undertaken (Weisstein,1974; Stevens,1971). Whilst relatively simple in character, magnitude estimation has been shown to produce a similar masking function to that obtained with a more rigorous psychophysical techniques (Weisstein,1974), and has the advantage of being a relatively straightforward procedure.

Six subjects were used in the magnitude estimation experiment, one of whom was also a subject in the VEP experiment. A modulus of ten was used, this value being given to the target stimulus when presented alone. The subject's task was to assign a value between ten and zero to the contrast of the target when succeeded by the masking stimulus over a range of SOAs. Five such ratings were taken at each randomly determined SOA, the subject first being presented with the target stimulus alone, and then with the target/mask combination at the appropriate SOA. When subjects were unable to assign a value on any particular run, the sequence was repeated.

The procedure for the VEP experiment and the method of calculating percentage peak amplitude were the same as used in chapter 4. Three subjects were used.

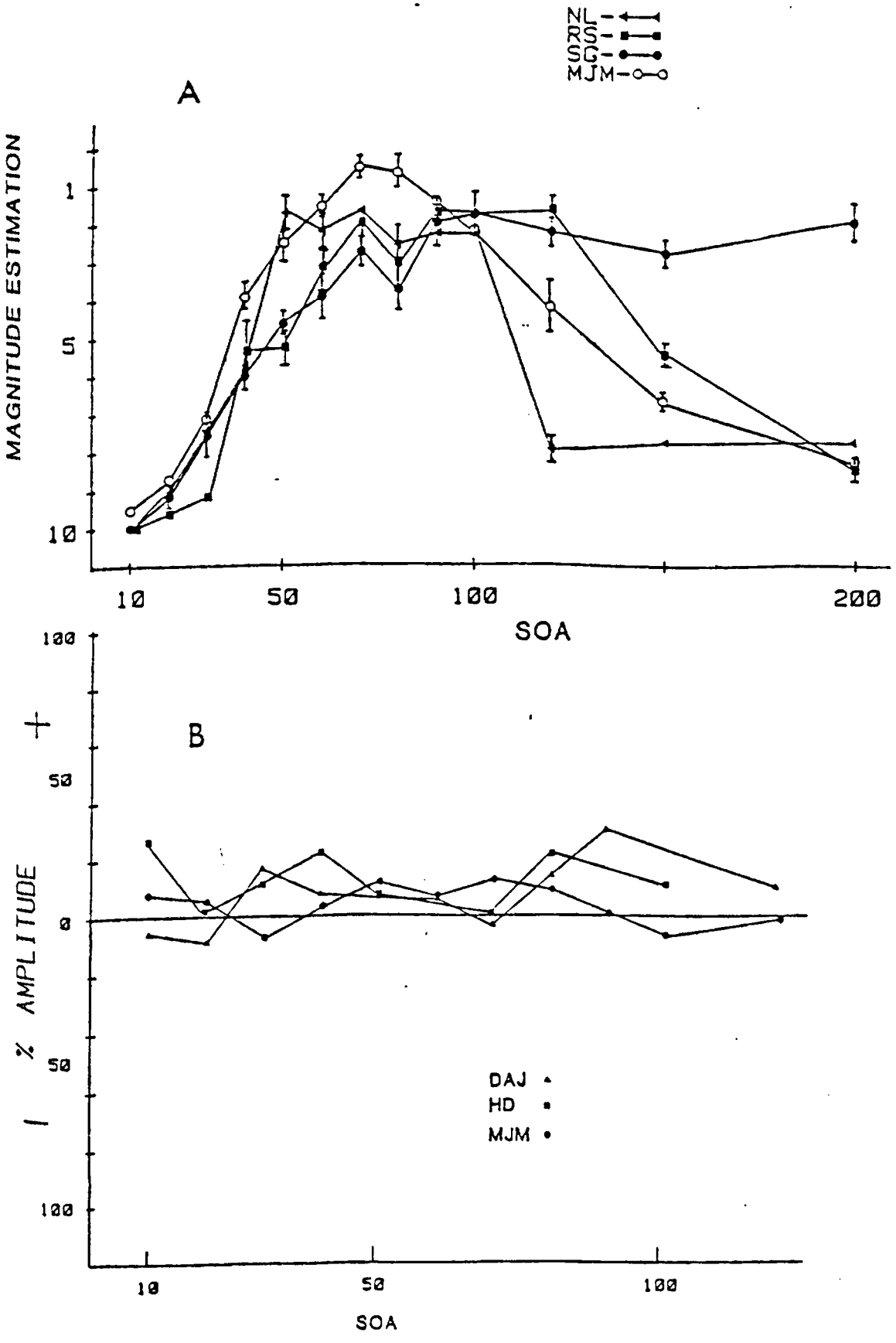


Figure 8.4

The form of the psychophysical masking functions. Each point represents the mean of four trials at each SOA. A value of 10 on the magnitude scale means that the there is no subjective attenuation of target contrast. See text for further explanation.

Target VEP amplitude plotted as a function of SOA. Data for three subjects. The amplitude of the target VEP is plotted as a percentage of the amplitude of the VEP elicited in the non-masked condition.

8.3:- VEP and Psychophysical Results

The results of the magnitude estimation experiment are presented in figure 8.4a the function obtained under these conditions is similar to the typical inverted 'U' shaped function reported by other workers (see Weisstein,1973). Subject SG however shows an extended masking function. Post experimental questioning revealed that this subject experienced considerable difficulty in distinguishing the target from the mask, as a result of pronounced apparent motion.

The masking of the target stimulus was not however mirrored by the any attenuation of the VEP, as can be seen from figure 8.5a-b where typical waveforms for three subjects have been presented. At short (10-30 msec) SOAs, the range over which subjective masking does not occur, the response to both target and mask overlap temporally; indeed there is a slight increase in the latency of the peak (approximately 5-7 msec) at SOAs of 20 msec, suggesting that the 'peak' at this interval reflects the combined contribution of neuronal mechanisms independently stimulated by the two stimuli.

However by 30 msec SOA, the response to the mask begins to separate from that to the target, and by 50 msec is well clear from it, growing in amplitude as the SOA is progressively increased. The important and significant point is that over the range of SOAs for which subjective masking is maximal the VEP elicited by the perceptually masked target shows no evidence of attenuation.

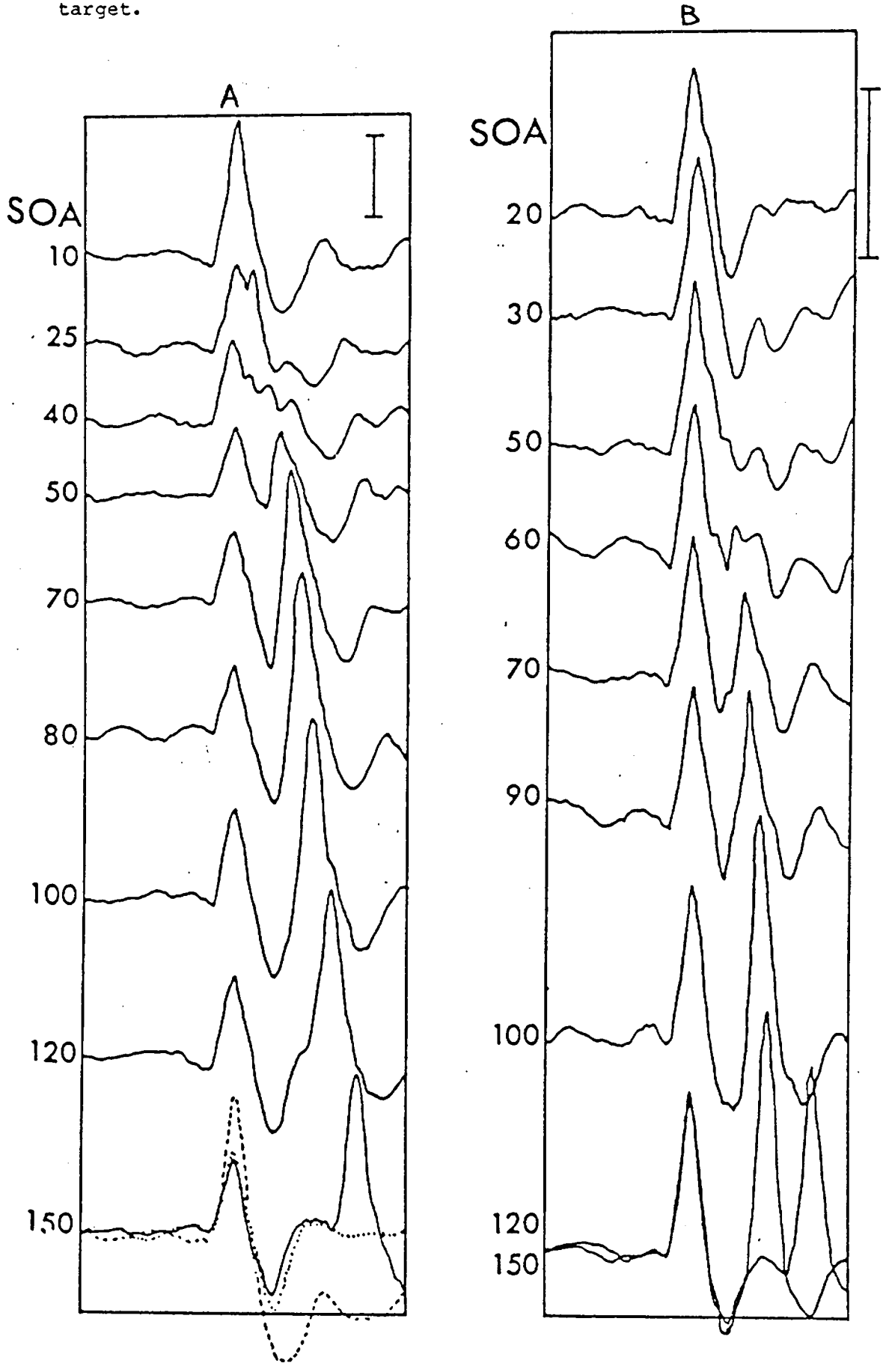
In figure 8.4b the amplitude of the combined response for short SOAs, or the isolated response to the target stimulus for SOAs greater than the limit of temporal resolution has been plotted as a percentage of the potential evoked by the latter when presented alone. This figure clearly indicates the dissociation between the electrophysiological responses and the psychophysical measures of masking.

The waveforms shown in figure 8.6, obtained with positive contrast stimuli, and show that under these conditions also the amplitude of the VEP to the perceptually masked target is never attenuated. The time course of the VEPs are similar to those recorded with the negative contrast pattern.

8.4. Experiment 8.2:- Disc-annulus metacontrast.

Figure 8.5a

VEPs for two subjects recorded under metacontrast masking. In column A the dashed waveform was elicited by the masking stimulus presented by itself, and the dotted waveform by the target.



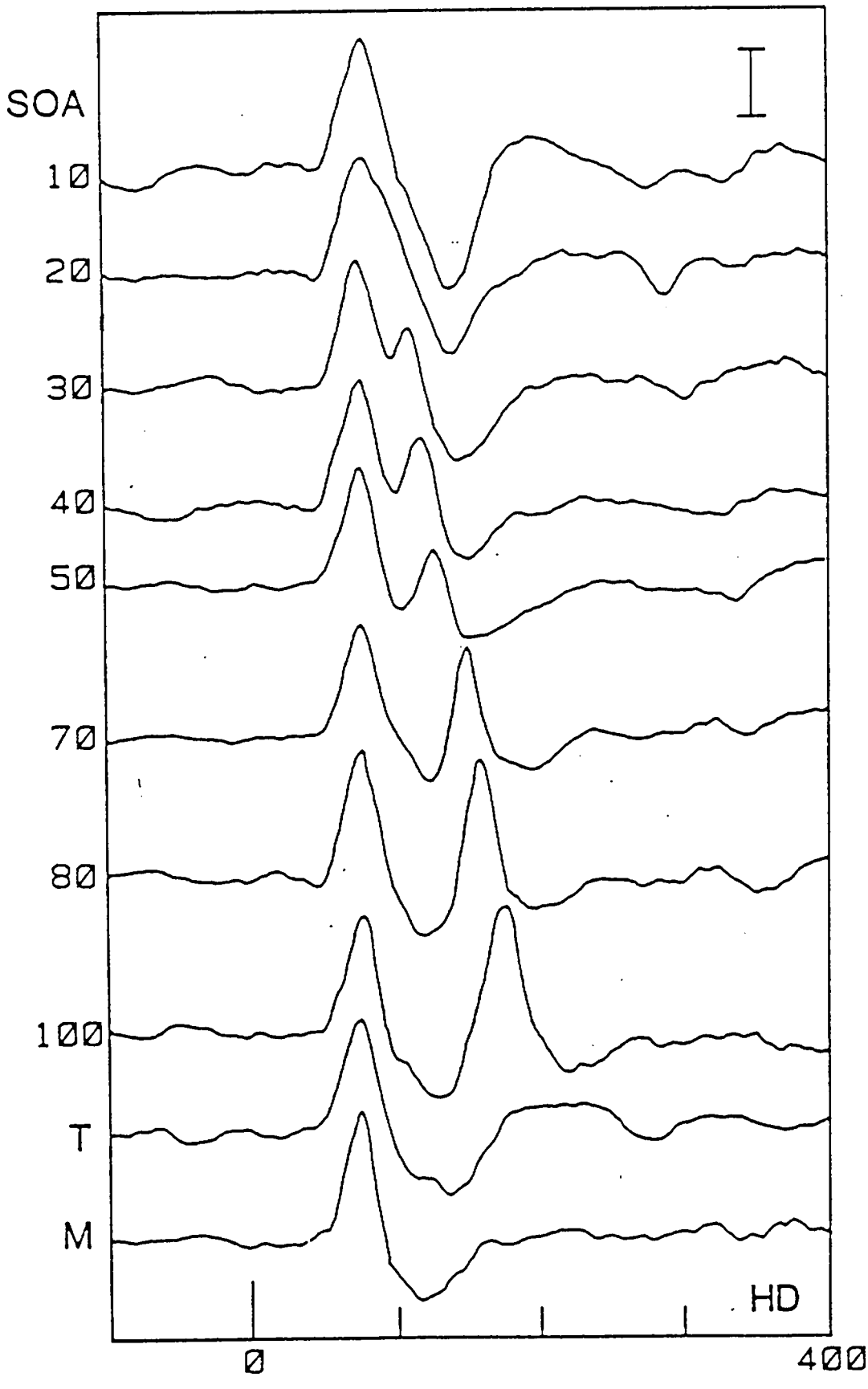


Figure 8.5b

VEPs for a third subject elicited under metacontrast masking.

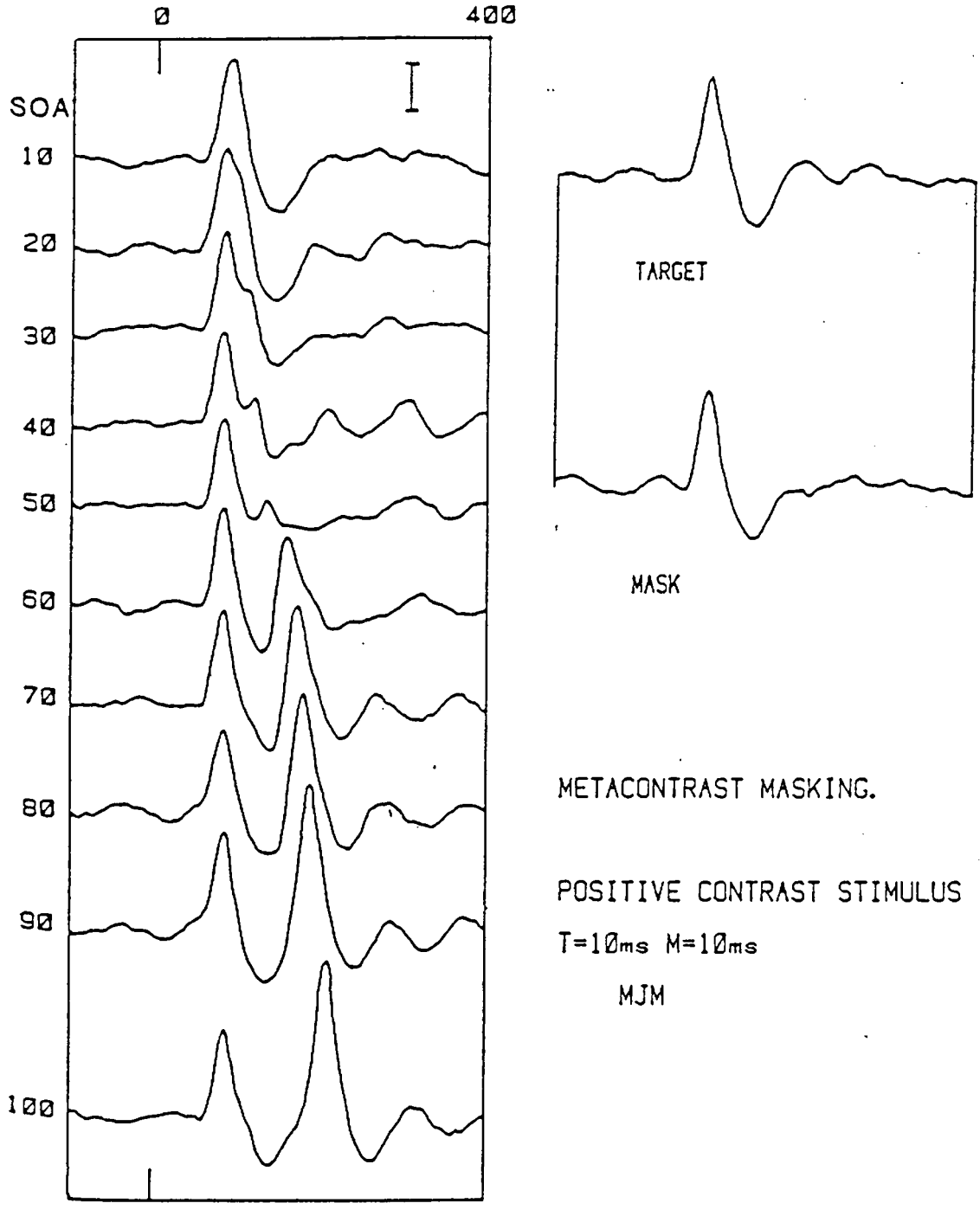


Figure 8.6

Waveforms for M.J.M. obtained under positive contrast target and mask conditions.

Methods and Procedure

The target stimulus used in this experiment was a matrix of full contrast squares, each square subtending 16x16'arc with a duration of 10 msec. They were well above threshold.

The masking stimulus was the outline stimulus of the above pattern. The line width of the outline pattern had a width of 1.0'arc and was exactly aligned with the contrast squares. The duration of the mask was 40 msec, and although psychophysical tests of the extent of metacontrast under these conditions it was found that subjects were unable to detect the target for SOAs of 25-100 msec. Indeed at the end of the experiments both naive subjects, DAJ and HD, had no knowledge that the target had ever been presented during the masking trials.

Three subjects were again used.

Results

In figure 8.7 are shown the VEPs recorded in two subjects.

It is quite evident that for the range of SOAs over which the target is completely masked perceptually, the response of the striate cortex, as reflected in the amplitude of the CI component, shows no evidence of attenuation. The target VEP remains constant in latency and amplitude. It appears therefore that the properties of CI do not correlate with metacontrast phenomena as produced by concentric targets and masks.

Consistent with the data reported later and in chapter 6 the peak latency of the component elicited by the mask (outline) stimulus is some 15-20 msec longer than that produced with full contrast square, when each is presented independently.

Experiment 8.3. Procedure

In this experiment the classic disc/annulus paradigm was again used as a final check against the possibility that the slightly novel stimulus paradigms used here mitigate against the observation of VEP correlates of metacontrast.

The stimulus configuration used is shown in figure 8.8; each stimulus had a duration of 10 msec. The target was 12'arc side length and there was no spatial separation between the inner border of the mask and the outer boarder of the target. One subject was used.

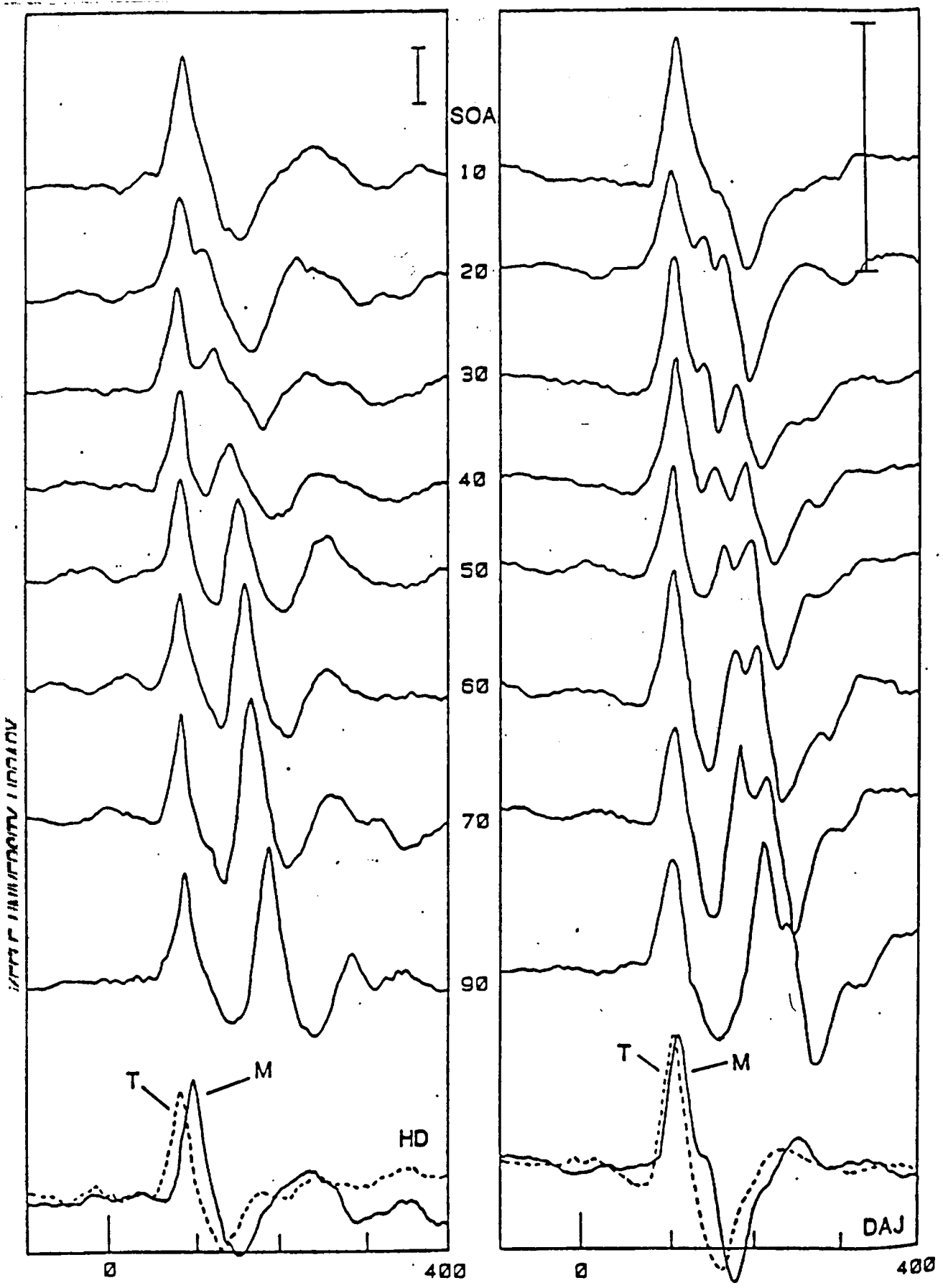


Figure 8.7

Waveforms obtained in experiment 2 for three subjects. The target is subjectively masked for SOAs up to 100 msec under these conditions. The latency of the response to this particular masking stimulus is longer than that of the target when both are presented independently as is shown at the bottom of each column. These data are consistent in turn with those presented in chapters 6, 7 and 13. The response to the higher spatial frequency mask being longer than that of the lower frequency target will be relatively more delayed at short SOAs compared to stimuli with the same spatial frequency.

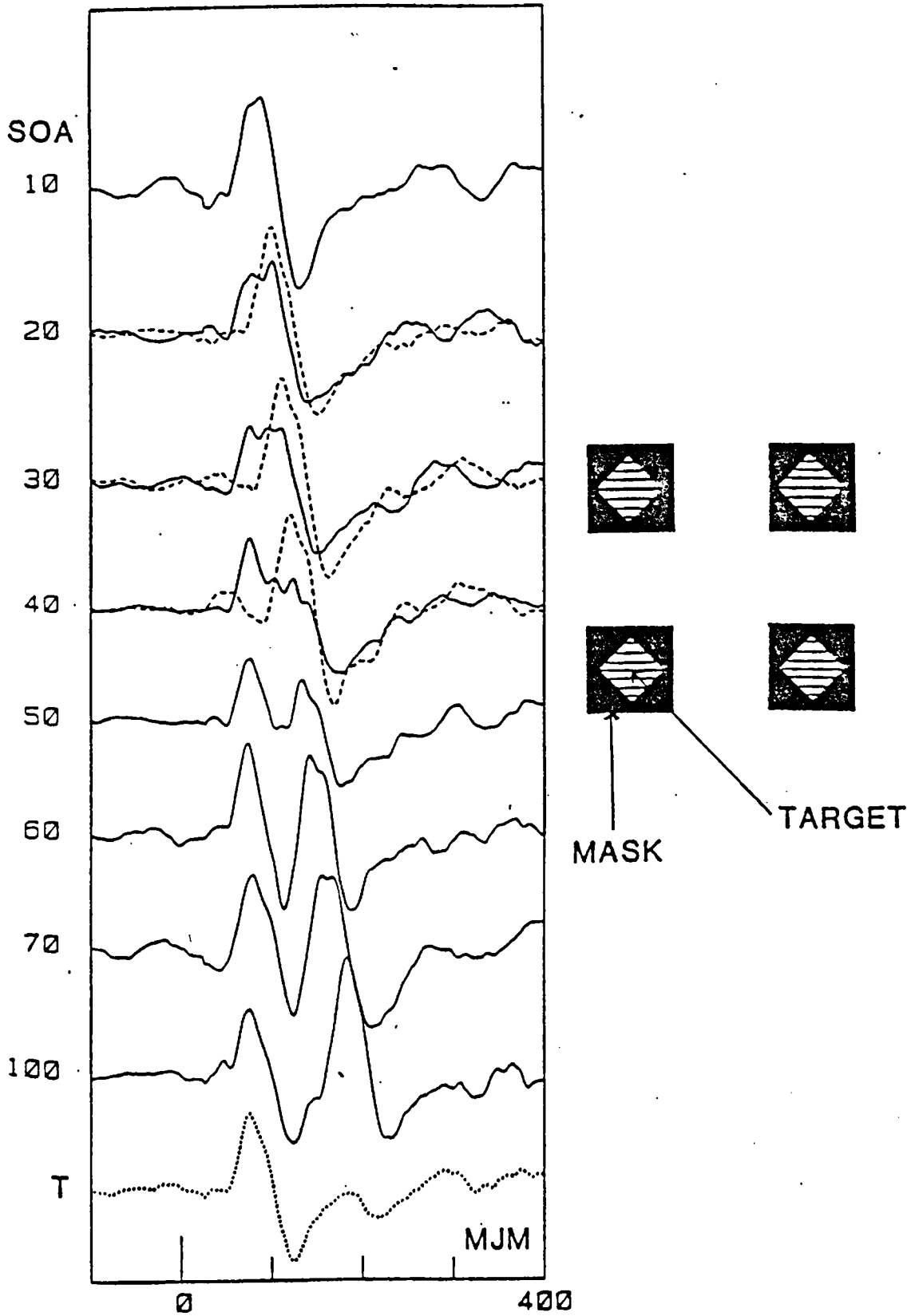


Figure 8.8

Illustrates the form of the target and mask and also the waveforms elicited by them. The continuous trace is the waveform elicited by the target+mask, the dotted trace at the bottom of the column was evoked by the target presented alone. the absence of the target. These waveform indicates that the latency of mask activity is independent of the occurrence of the target but that its amplitude is reduced at short SOAs, presumably because of its temoral overlap with the negative potential on the trailing edge of CI, evident in the VEP elicited by the target presented by itself.

When the amplitude of the target VEP is plotted as a function of SOA it is found that there is no evidence of amplitude attenuation.

Results

The waveforms obtained in this experiment are shown in figure 8.8 and it is clear that the trend in the waveforms is similar to that reported in experiments 8.1 and 8.2. At short intervals, the potentials overlap temporally; by 20-30 msec SOA, the response to the outer annulus separates from that to the inner target. At all SOAs greater than 40 msec, the response to the masking stimulus is separate from that to the target, and the potential evoked by the latter showing no evidence of attenuation despite the fact that for SOAs of 20-100 msec, the target remains undetected. Indeed at short interval brightness enhancement occurs, but in the opposite direction, so that the region of the target appears brighter than the background field, allthough it is physically darker.

Part II

8.5 Experiment 8.5:- Single element target and masks and CI

In the following experiments VEPs were recorded to a stimulus paradigm more commonly used in psychophysical studies of metacontrast, (see Kahneman,1968). It is difficult to undertake such experiments because a decrease in the number of contrast borders within a stimulus increases the signal-to-noise ratio, which makes accurate quantification of the resultant potential a dubious procedure. However in some subjects large and repeatable signals can be elicited by a brief stimulus containing just a single pattern element such as a square subtending some 12'arc within the foveal region of the field.

Foveal metacontrast has been reported to be weak or non-existent (Alpern,(1953). Indeed Breitmeyer & Ganz (1976) have noted that this feature would be consistent with their model because transient channels (and their assumed 'Y' cell neural substrate) are relatively absent from the fovea and thus the predicted interactions between them and the sustained channels cannot occur. The extent to which metacontrast will occur appears to be dependent upon the size and separation between stimuli (Saunders,1977; Lyon,1980). The stimuli used by Alpern (1953) (see figure 8.1), subtended 2.5 degrees along their vertical axes and, even under the smallest target/mask separation, the combined display would have subtended a visual angle of some 2 x 2.5 degrees in the lower half-field. As Lyon et al (1980) have shown, stimulus

configurations that produce pronounced parafoveal metacontrast result in weak foveal metacontrast.

Whilst is is easier to use the same stimulus configurations in different retinal areas, the most meaningful comparison between functions obtained in different regions of the visual field must be made between stimuli optimal for each. Thus Lyon et al (1980) have shown that foveal metacontrast can be observed to the same extent and with the same time course as that reported at para and peripheral sites and the stimuli used in the following experiments produced such masking effects.

Methods

The squares were in this case outline squares with a line width of 1.2'arc and a side length of 24'arc. The stimuli were positioned such that the edge of the nearest mask element was 8'arc from the centre of the fixation cross (see figure 8.9a-b). There was a 4'arc seperation between the contours of the target and the flanking mask squares. Stimulus duration was 20 msec.

Results

In figure 8.10 the amplitude of CI elicted by the target stimulus over the range of SOAs has been plotted as a percentage of the response to the target presented alone. In figure 8.9 typical waveforms obtained from both subjects under the present conditions. It is clear from both figures that over the range of SOAs that produce complete subjective masking the VEP elicited by the target stimulus clearly shows no evidence of attenuation.

It is concluded therefore that under conditions which are commonly reported to produce metacontrast there is no electrophysiological evidence which would suggest an inhibitory interaction within the striate cortex of man.

8.6. Experiment 8.5:- Single element metacontrast and CII

Before the implications of these results are considered in relation to the theories previously outlined, the possibility that metacontrast phenomena result from interactions within the visual areas of extrastriate cortex must be considered.

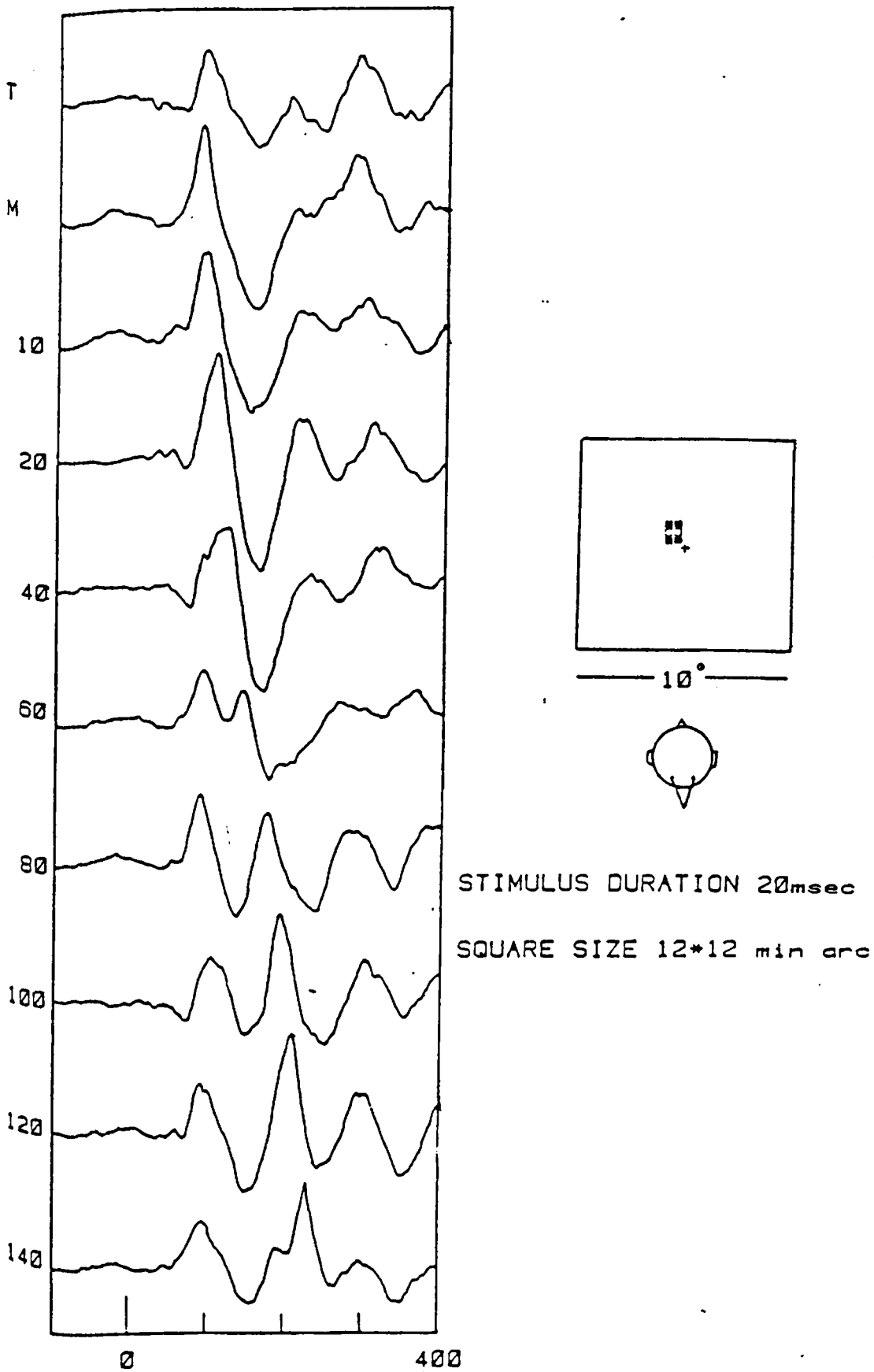


Figure 8.9a

VEPs recorded for the single element target/mask combinations. The size of each square is given in each figure.

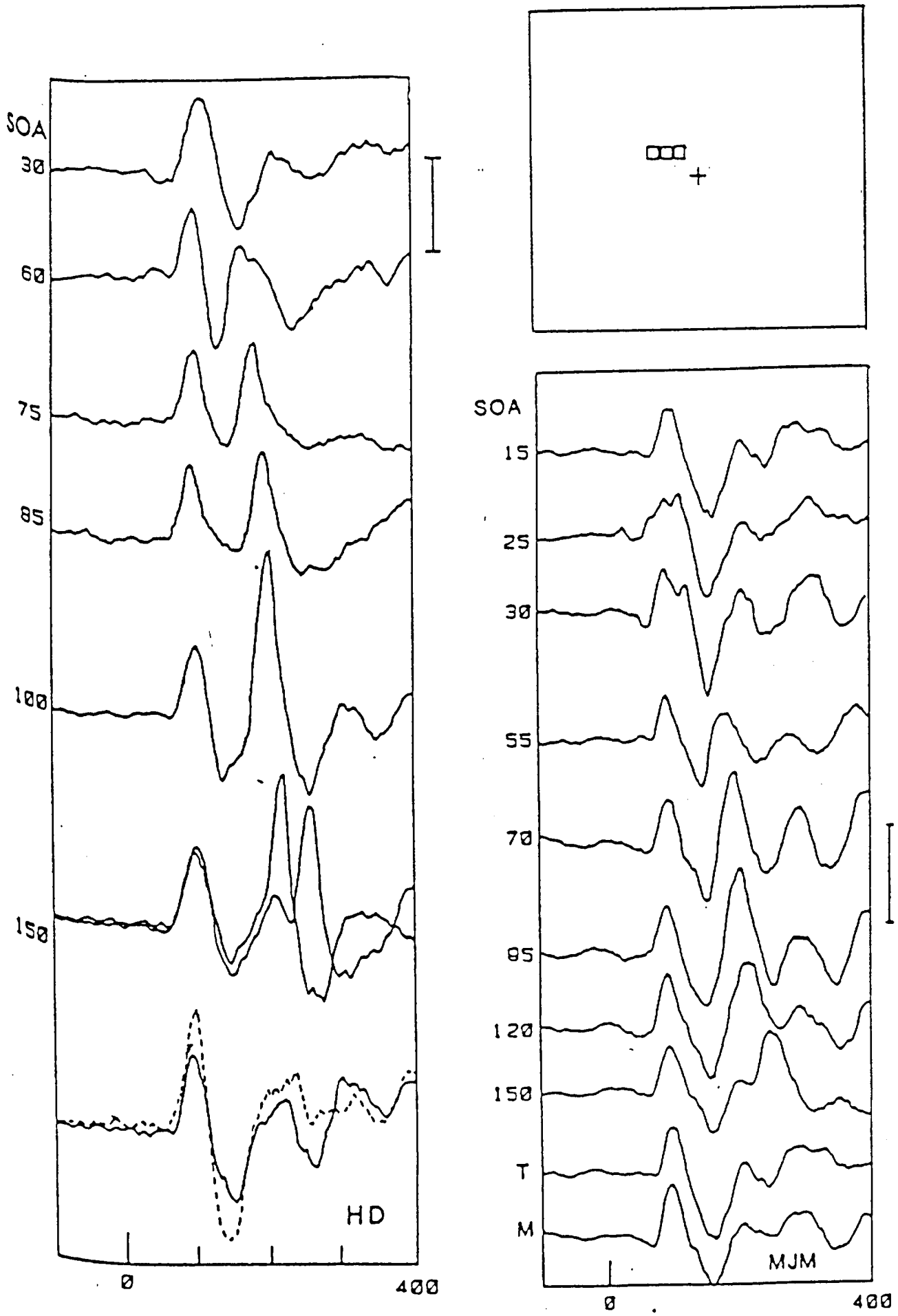
Under these conditions target masking is complete at SOAs between 40-100 msec SOA (this phenomena is easily verified with tachistoscopic presentation).

The stimuli used here were contrast squares as oppossed to outline square, the target stimulus is shown as outlines merely for convenience.

Figure 3.9b

VEP recorded under conditions that replicate Kahnemans stimulus paradigm.

The size of these stimuli would be optimal to activate the postulated sustained channels.



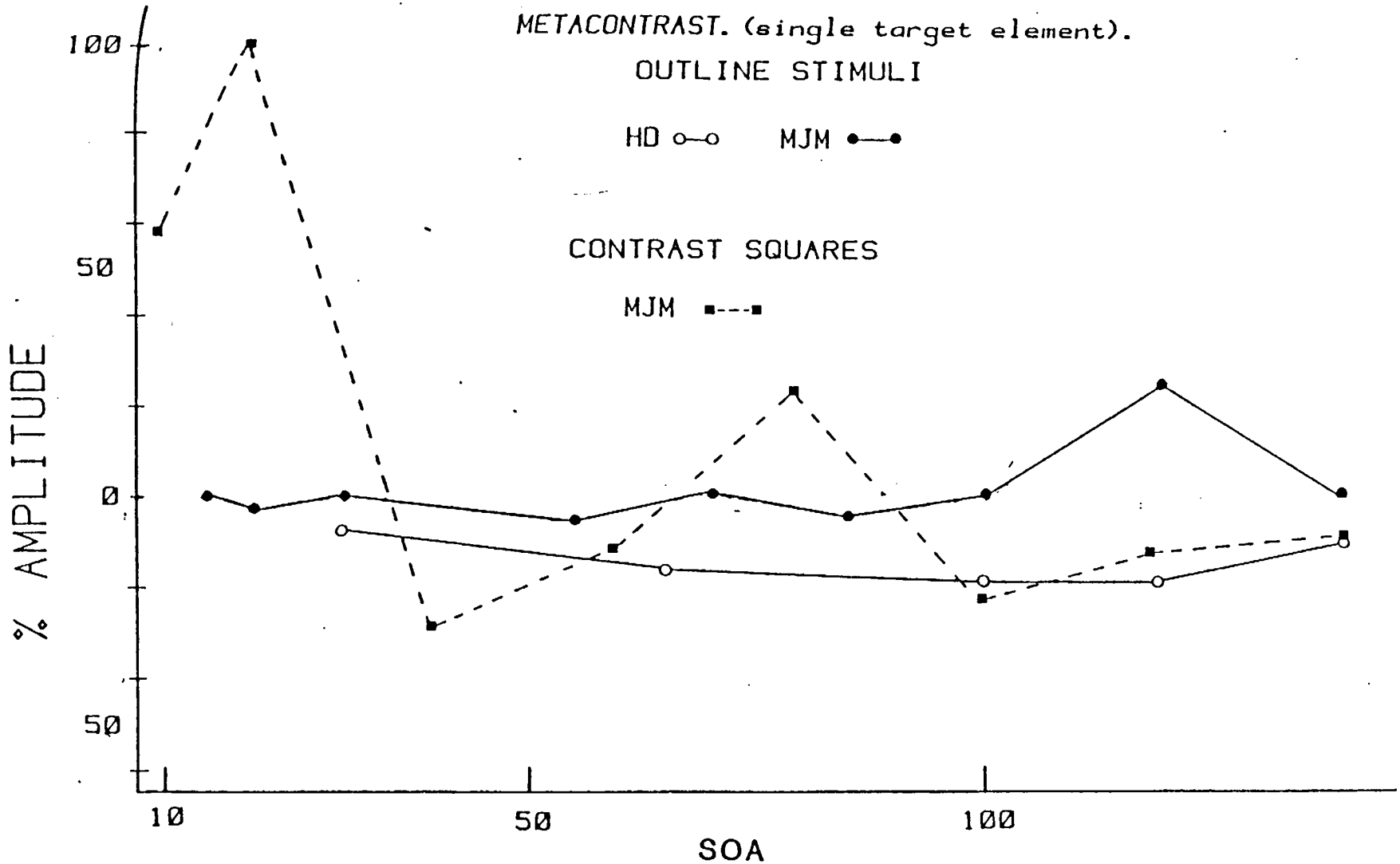


Figure 8.10

Plots of target VEP amplitude as a function of SOA under single element masking conditions.

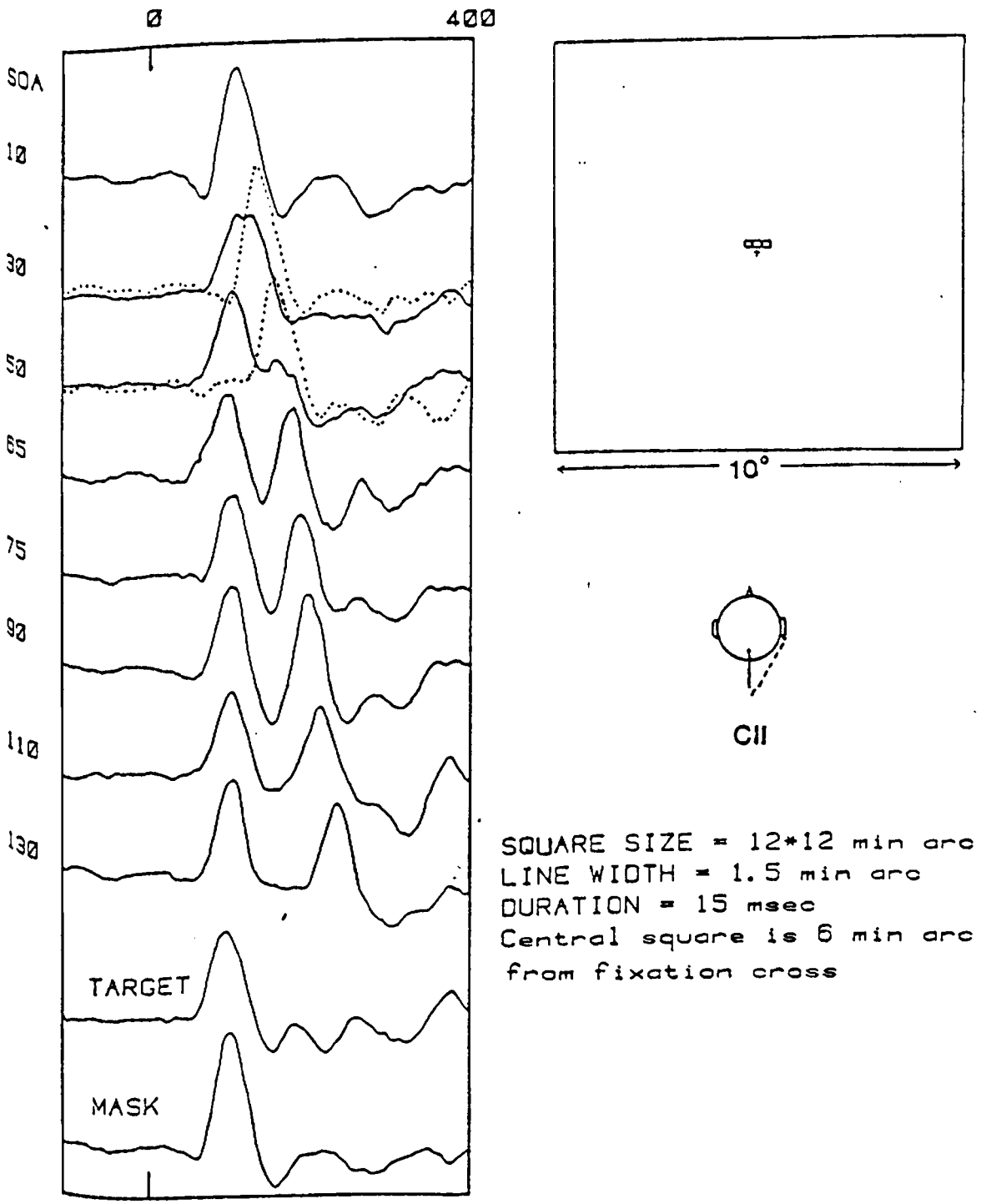


Figure 8.11

CII elicited by single element stimuli. The continuous trace is the waveform recorded by the target & mask, that of the dotted trace elicited by the mask stimulus presented in the absence of the target at the appropriate onset interval. As with previous studies the combination of these stimuli produce complete masking for SOAs between 40-120 msec.

From a consideration of their respective properties it might be predicted that of the two, there would be greater likelihood of the CII component showing evidence of response interaction under a metacontrast paradigm than CI. The phenomena is essentially one of contour interaction (Kohlers,1958; Weisstein,1973) and Jeffreys (1979) has suggested that the CII component probably reflects activity from within a region of extrastriate cortex exclusively sensitive to the boundary contours of visual stimuli.

Preliminary experiments by Jeffreys (personal communication) had suggested that under a metacontrast paradigm CII is similarly unaffected over a range of onset intervals that produce subjective masking. In order to extend the implications of the previous experiments I decided to examine in more detail the properties of this component over a more extensive range of SOAs with stimuli that have been shown to produce metacontrast.

One subject was used. Stimuli were small outline squares, as shown in figure 8.11 presented for 10 msec. There was no separation between the contours of the target and its flanking mask, the side length of which was 12'arc and line width 1.2'arc. To record CII the stimulus was presented above the fixation cross, and the VEPs recorded from a midline electrode 4 cm above the inion with reference to the right ear.

Results

Figure 8.11 shows the waveforms recorded. The dashed trace was elicited by the mask stimulus presented by itself at the appropriate SOA and indicates the constant latency of the response to these stimuli. For the range of SOAs between 50-120 msec the target stimulus is subjectively masked; there is, however, no evidence of amplitude attenuation for CII over this range. Thus, there is no evidence of response interactions within the extrastriate cortex which would correlate with the metacontrast phemonomenon. It should be noted that these outline stimuli produce complete perceptual masking, rather than simple contrast reduction as observed in experiment 1 with full contrast squares.

8.7. General Discussion

The results of these experiments have shown that there is no property of either the CI or CII components which correlates with the phenomena of metacontrast. It can be concluded, therefore, that if the model of Jeffreys & Axford (1972) for the source locus of these components is correct, then the phenomena does not result from inhibitory neural interactions within either the striate or in regions of extrastriate cortex, as implied in the models of Weisstein (1968,1973,1975) and Breitmeyer & Ganz (1976) or Martin (1973).

Before the implications of these results are considered in relation to other electrophysiological data, two possible objections to the assumptions underlying these experiments need to be considered. They are :-

A:- that the properties of the pattern-specific components bear little relationship to subjective sensation.

and

B:- that metacontrast phenomena are the result of neural interactions within the primary visual cortex, but that these interactions are more subtle than would be revealed by gross electrophysiological recording. It, has for example, been suggested by MacKay (personal communication) that the phenomena might be determined by a 'misinterpretation' of the physiological signal evoked by the target within the neural array, rather than by any decrease in its excitatory potential per se.

These problems are obviously related. However the implication of the notion expressed in the second objection are far reaching for, not only would one need to know in detail the pattern of neural activity within each region of visual cortex for which the target is an effective stimulus, in order to chart possible variations in this activity as a function of the subsequent presentation of the mask, but one would also have to specify for each aspect of the neural response, a specific relationship to some aspect of the target's physical features. Moreover, knowing the variations in the intensity and latency of neural responses that were dependent on the temporal variations of the target and masking stimulus would not leave one in a position to specify a neural correlate of the phenomenon as the aspect of greatest importance may be the timing of specific activity on a relative, rather than absolute basis. Logically however, one must, I believe, concede that from a consideration of neural conduction velocity alone it is unlikely that the neural representation of the target stimulus could be 'interfered' with by a stimulus presented some 30-40 msec after the

first signs of unit discharge produced by the former are observed within the striate cortex. [Assuming a latency of 70 msec from the onset of brief visual stimulus of medium to high contrast to the latency of peak impluse discharge of striate cells, see figure chapter 3].

If one further accepts that the latency of excitatory synaptic potentials recorded by Mitzdorf & Singer (1979) between area 17 and 18 of the macaque would be little altered by visual, as opposed to electrical, stimulation of the primary afferents, then one might add a further 10-15 msec to the overall retino-striate latency value to arrive at a figure which would then include most of the extrastriate visual areas (see chapter 1 section 1.3 which suggests similar values for the monkey VEP).

It is clear therefore that, as the normative peak latency value of CII implies, a briefly presented stimulus will have evoked unit discharges within most of the major functional visual areas before the presentation of the stimulus that completely masks it perceptually. Unless, as indeed Bridgeman (1975) has suggested (see below) further stimulus processing takes place at the same cortical site, but at a 'later' time, rather than (as might be expected from the overall pattern of afferent connections) at a higher cortical level at a later time (see below), it would seem that whatever the relationship between 'information' content and the stimulus specific afferent volley to cortex, the phenomenon of metacontrast cannot logically be explained in terms of neural interactions at this level.

With regard to objection A, the data reported in chapters 3 to 6 have shown a very close relationship between some of the temporally dependent properties of CI and CII and the psychophysical counterparts. Where this correlation breaks down, as in the present case, this cannot itself question the significance of VEPs as indices of neural activity. Rather, the VEP data questions the above mentioned explanation of psychophysical phenomena in terms physiological mechanism.

The model of metacontrast as proposed by Weisstein (1973) would seem to be invalid. There is no evidence of the predicted 'fast' inhibition (Baker et al,1969; Wanetabe et al,1966). This has recently led Weisstein (1975) to modify her original model by incorporating the properties of the sustained and transient channels into the equations of the two factor neuron, since she writes, "that for the model to

Figure 8.12

Single unit data from Shiller (1969) and Bridgman (1975). In Bridgmans experiment the stimuli were bars, as shown in the top left of the figure. See text for discussion.

work, the only thing that needs to be fast is a fast excitatory response which will inhibit a slow excitatory response". Whilst such may be the case the available physiological evidence would suggest that the sustained ('X') and transient ('Y') neurons do not have these relevant properties (see Lennie,1980).

Relationship to other electrophysiological studies

Those previous studies which have sought VEP correlates of metacontrast have been discussed above and, because of their inherent limitations as VEP studies, they will not be considered any further beyond noting that only the findings of Schiller & Chorover (1966) are consistent with the present data.

A number of single unit studies have also sought physiological correlates of metacontrast at various levels of the cat visual system, although that of Schiller (1969) was the only one that has used a stimulus configuration known to give rise to compelling metacontrast in man (see figure 8.12) Bridgeman (1975), who conducted a more detailed study at the retinal, lateral geniculate and cortical level, had used stimuli that are more commonly used in the study of apparent motion. Whereas Schiller had used the classic disc/annulus configuration, with the disc presented to the centre of the receptive field and the masking annulus to the inhibitory surround, Bridgeman had used two short adjoining contrast bars briefly presented to the centre of the receptive field. As is easily verified, such stimuli give rise to the phenomenon of apparent motion. The justification for their use was that in the more classic flanking target/mask configuration some apparent motion can be observed at certain SOAs (Weisstein,1973). However, as Kolers (1962) has shown, apparent motion and metacontrast appear to be distinct phenomena, each of which can be observed independently and are governed by different features (see Weisstein,1973). For example, apparent motion can be perceived between a perceptually masked (flanked) stimulus and a stimulus external to the flanking masker as shown by Kolers (1962). [See however Kahneman (1967)].

The weight of psychophysical evidence points to two distinct phenomena: metacontrast being a case of diminishing target contrast dependent on the close spatial contiguity of a target and masker in patterns of similar 'form' whilst apparent motion can occur between any two briefly presented non-spatially contiguous stimuli and is essentially independent of their spatial properties.

Schiller (1967) did not find a single unit correlate of metacontrast: at all SOAs for which the target was subjectively masked (as judged by the experimenter), units within the layer A of the cat LGN could be shown to respond to the target (see figure 8.12). At short SOAs (below 10 msec), the response exhibited non-linear interaction as the input to the inhibitory surround depressed the excitatory centre.

The data reported by Bridgeman are perhaps more interesting, and are taken as showing a simple neural correlate of metacontrast (Foster & Mason, 1979).

Bridgeman divided the population of cells studied into two classes:-

Class A:- these cells showed an initial excitatory response occurring some 60 msec after stimulus onset followed by a gradual decline in discharge level.

Class B:- these cells had an initial excitatory response at 60 msec after stimulus onset, followed however, at some 200 msec post stimulus onset by a second excitatory response. Such cells were not exclusive to the visual cortex, and were observed also in the LGN.

Figure 8.13 is taken from Bridgeman (1975) and illustrates a curious argument. For class B cells, the initial response shows no evidence of attenuation, although there is a slight decrease in amplitude at zero SOAs. However the late response of this class shows response attenuation which is maximal at both +- 60 msec SOAs, ie the onset interval at which metacontrast is commonly reported to be most pronounced. Thus Bridgeman suggests that such cells may play a role in metacontrast masking. For class A cells, which have no late excitatory response, the initial excitatory response showed little attenuation and thus had properties that did not correlate with metacontrast. However the late response of this class had, in contrast to class B, a monotonic response function, maximal at zero SOAs. Class A cells were not considered to have properties consistent with a role in determining the psychophysically observed metacontrast phenomena.

However, a cell either has a late response or it does not. To measure some aspect of a response which, by definition, is determined not to occur is curious, if not illogical. In the present case the limited illustration of post stimulus time histograms does in fact suggest that the amplitude of the smallest late peak in the class B group is no greater than the noise level. For those cells defined as

Figure 8.13

The data for Bridgeman (1975) showing examples of response functions observed for the class A and B cells described in the text.

For the striate cells 'with' the late response there is a non-monotonic response attenuation for the late response which is maximal at -60 and +60 msec SOA (see text for discussion).

For the striate 'late' peak group there is no attenuation of the 'early' response, as shown by the open symbols in the bottom left figure.

The 'without' late peak group illustrated at the bottom-most left graph, the early response shows little evidence of a response.

class A the peak measured by Bridgeman must in fact have been no greater than background level, otherwise it would have been a class B cell.

The aspect of the response of group B cells that does appear to show attenuation at metacontrast intervals is the late responses evoked by both stimuli. As indeed both stimuli are similar in all aspect, except their position on the receptive field, and because no psychophysical data was reported to indicate whether S1 had been masked by S2 or S2 by S1, it is totally arbitrary to have plotted the response to S1 as a function of SOA and then to claim neural correlates of metacontrast.

Bridgemans data is, at best, in need of replication. To have drawn the further comparison between other reported electrophysiological correlates of masking phenomena is similarly unwarranted. The correspondence between the late peak of these single cells and the 200 msec latency VEP recorded by Vaughan & Silverstein (1968) is probably coincidental, since in the latter study no attempt was made to show that this VEP was not composite, which is likely since full field stimulation was used, and no attempt was made to determine the site of its generators.

8.8. Summary

The fundamental basis of the 'sustained/transient' model of metacontrast is that the retino-striate pathways in man contain two distinct information processing channels with latency differnces of between 70-120 msec. The VEP data presented in this chapter, and in chapter 7 have not supported this prediction.

Recent psychophysical data questions either the existence of the socalled sustained/transient channel dichotomy or alternatively their role in metacontrast masking. Bowen et al (1977) have argued that there are tonic and phasic neural channels which carry chromatic and achromatic information respectively (see Inling & Drum,1973). If as Breitmeyer & Ganz (1976) suggest, metacontrast depends on the interaction between 'slow' and 'fast' channels, and if the latter are identical to the former, then metacontrast would not be expected to occur between targets and masks differing in chromaticity alone since they will only stimulate the sustained (chromatic) channels. Evidence has indeed suggested that this was the case (see Breitmeyer &

Ganz,1976).

However Reeves (1981) has reported metacontrast interactions between stimuli differing only in hue, a result which implies that either there are no latency differences between so called 'fast' and 'slow' channels, or that the shorter latency, phasic, channel must be capable of carrying chromatic information. Acceptance of either of the above conclusions would necessitate a revision of the current conception of the properties of these postulated channels, or indeed of their existence (see also Foster,1978).

The VEP data suggest metacontrast is unlikely to have any simple relationship with interactions at a purely 'visual' level of representation, as Kolers (1962) concluded from a consideration of the spatio-temporal properties of the phenomena.

Chapter 9: Visual noise masking

Introduction

It has been suggested that visual noise masking, in common with other types of masking phenomena produced by "spatially contiguous" stimuli (Kinsbourne & Warrington,1962; Weisstein,1973; Sperling,1965; Breitmeyer & Ganz,1976; Turvey,1973), reflect some form of interaction within the visual system, at either a peripheral or central level, (see Coltheart,1980).

The masking functions produced by these spatially contiguous stimuli are typically monotonic (type A), as indicated in figure 8.2b, of chapter 8. The experiments reported in this chapter, which is divided into two main parts, will investigate possible neural correlates of these masking functions. In part I, the CI component will be studied under a forward, backward and dichoptic visual noise masking paradigm and the findings related to comparable experiments on single units in the monkey's striate cortex. In part II the CII component will be studied under a backward masking paradigm and electrophysiological correlates of these types of masking phenomena will described.

Prior to a more detailed disscussion of the phenomena a distinction must be made between the various stimulus paradigms that produce type 'A' functions, for although the functions may appear to be similar in a number of cases the mechanisms that determine them must be expected to differ, given the widely disparate paradigms under which they are reported. This will in turn affect the implications which can be drawn from the following experiments.

It has been suggested (Crawford,1947; Sperling,1965) that masking by light, where a brief spot of light presented at threshold is preceded or succeeded by an intense masking flash, spatially contiguous with and surrounding it, is the result of neuronal interactions within the retina. These effects do not show inter-ocular transfer (Kahneman,1967) and there is both evoked potential and single unit data indicating a decreased responsiveness of the system to the perceptually masked target. Schiller (1968), recording from layer A of the cat LGN reported that brief threshold spots of light presented to the centre of the receptive field of cells within that body failed to produce impulse responses when followed at some critical interval by a higher intensity

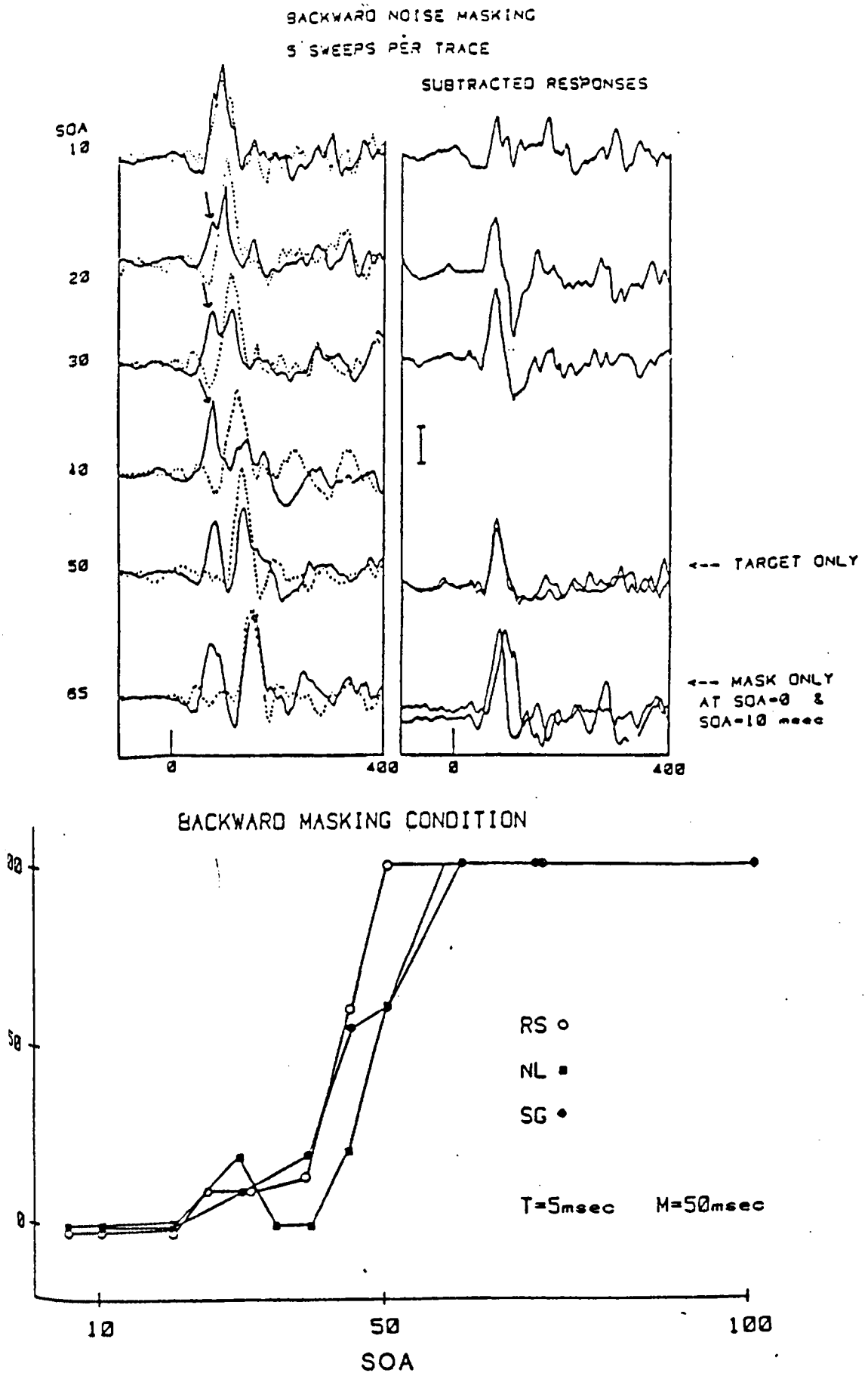


Figure 9.1.

A:- VEPs recorded to five stimulus presentations. The waveforms in column B are obtained by subtracting the mask VEP from the target+mask VEPs which are shown in column A.

B:- Percentage correct detection scores for three subjects under backward masking conditions. Each point is the mean of four trials.

spot (3 log units above unit threshold) which covered both the excitatory centre and inhibitory surround. Such interactions were attributed to the relative decrease in response latency of activity evoked by the higher intensity mask.

Donchin et al (1965) has offered a similar explanation to account for the target/mask interactions revealed in a VEP study of light masking. Whilst the subtraction procedure used by Donchin et al is open to question because it assumes complete linearity of response, the consistency of their results with those of Schiller does indeed suggest that a "neural overtake" model such as proposed by Crawford (1947) could indeed explain most, if not all, the experimental data for this type masking phenomena. The impulse response of the system (see chapter 3 and 7) depends critically upon stimulus intensity and adaptation level (Levick & Zacks,1970; and Gouras & Link (1967). Similarly it has also been shown (see chapter 3 and 7) that the latency of these pattern specific VEP components is dependent not only upon the spatial frequency or angular subtense of the elements of a pattern but also on its physical contrast; the extent of the latency increase in the case of the latter being of equivalent order of magnitude to that reported for single units (Galletti et al,1979; Baker et al,1969).

There is little published data on the relationship between latency of discharge for single cells and the spatial frequency of the driving stimulus, although the available physiological and morphological data (see chapter 1) does indicate a relationship between receptive field size and axon width hence conduction velocity of the afferent fibers feeding them. Cells tuned to the higher frequencies had smaller receptive fields and would therefore be fed by slower afferents; the converse is true for cells with larger receptive fields.

The above considerations give a ready explanation to those reports of type 'A' masking functions obtained with patterned stimuli, where the masking stimulus is of greater physical contrast than the target However a distinction must be made not only between type 'A' effects produced by light (which indeed are by definition not pattern masking paradigms) but also between those effects produced by patterned stimuli having differing physical as opposed to the subjective contrast. It was shown in chapter 3, that the latencies of both the CI and CII components are independent of subjective contrast although this was not the case for the amplitude of the respective components.

9.1. Backward noise masking and CI

The aim of the following experiment was to determine the nature and extent of response interaction within the striate cortex produced under a backward noise masking paradigm.

A major criticism which can be made against most previous VEP studies of masking phenomena is that there has been little attempt to identify individual components as distinct from peaks of given polarity assumed to reflect stimulus processing within, what generally appears to have been considered a functionally homogeneous visual cortex.

A likely physiological correlate of perceptual masking has been assumed to be (Weisstein, 1973) a decreased responsivenes of postulated feature analysers predicted to mediate target detection; such analyzers are further assumed to be physiological mechanisms located within the visual cortex the activity of which should be recordable in the VEP. If true, then under conditions of target masking, the electrophysiological response of such feature detectors will be attenuated to some degree, and this will be reflected in the amplitude of the potential produced them. Whether the above assumption is justified can be decided only by experimentation. However an attenuated VEP, to a perceptually masked stimulus could be produced by interactions other than those of physiological origin, specifically non-linear interactions at the recording site. Therefore, before any VEP correlate of the subjective phenomena can be claimed, it must be shown that the VEP thought to be specifically evoked by the target is both

A:- a single component

and

B:- does not interact non-linearly with any potential evoked by the succeeding stimulus that perceptually masks it.

To my knowledge no study has attempted to do this. Instead most have used the method of response subtraction to assess the assumed physiological interactions. This method might be adequate if the VEP could be shown to be stable over time, but again (see Donchin et al, 1965), this has not been achieved and until it is, the method used in isolation must be considered a weak one. In the following study both the method of response subtraction and component isolation have been used.

Stimuli

The target consisted of a random pattern of squares, each subtending a visual angle of 12 x 12'arc. The masking stimulus was matrix of similar sized squares, computer generated and drawn by digital plotter to a black/white ratio of 40/50

9.2. Psychophysics:- Procedure

In order to make some comparison between the target/mask interactions observed at the electrophysiological level and that experienced subjectively a short psychophysical experiment was conducted to examine the extent of the masking interaction.

The stimulus configuration and duration were similar to those used in the VEP experiments; the temporal order being such as to produce backward masking.

Five subjects were used, all of whom were experienced observers. At each SOA, ranging in steps between 5 and 100 msec, subjects were presented with either the target and mask or with the mask stimulus alone, and their task was to press a response button to indicate whether they had or had not detected the target. Ten trials were undertaken at each randomly determined SOA. The subjects, fixated a small cross in the centre of the field and initiated the stimulus sequence by pressing a switch which, after 2 second, triggered the stimulus sequence.

Results

In figure 9.1 are plotted the percentage correct detection scores as a function of SOA. The results suggest that for SOAs up to 50 msec the target remains undetected; beyond this limit the detection score rise steeply to a point at approximately 60 msec where the target was detected on every presentation. The slope of the masking curve is similar to that reported in several more detailed studies of noise masking phenomena (Kinsbourne & Warrington,1962)

VEP Procedure

Three subjects were used in this study; the target was confined to the left half-field for two subjects and to the right half-field for the other. Four runs of 20 or 25 sweeps were undertaken.

At SOAs below 40 msec VEPs were also recorded to the masking stimulus presented alone at the appropriate onset delay, this

waveform was then subtracted off line from that elicited by both target and mask.

VEP Results

The VEPs obtained in this experiment have been shown in figures 9.2 & 9.3a for each of the three subjects. In all figures the waveforms shown in column B are those obtained from the subtraction of the dotted (mask alone) waveform from that of the full (target/mask) trace at the appropriate SOA. It is clear that the psychophysical and VEP data do not correlate. Despite between-subject differences in the absolute amplitude of the target VEP (see calibration bars), there is no evidence of response attenuation across the range of SOAs for which the target was shown to be undetected. This point is clear from the subtracted responses of subjects HD and MJM at SOAs of 30 msec and below, although for subject DAJ the lack of response attenuation can be observed in the unsubtracted waveforms even at the shortest SOA. For the former subjects the mask VEP does not separate from that to the target until SOAs of 15-20 msec. The reason for this difference is clear from an inspection of figures 9.3a where for two subjects the waveforms for independent stimulation of all the four quadrants and the half-fields have been presented along with the waveforms obtained when the VEPs from these quadrants are summed.

The main feature evident is that waveforms differ as a function of the independent half or quadrant-field stimulation with this electrode derivation and it can be seen that the response to each half-field is the sum of the two appropriate quadrants. Similarly the waveform obtained to full field stimulation can be derived from summing the waveform obtained to independent stimulation of the four quadrants. The important aspect for the present discussion is that, for both subjects, the contribution to CI comes predominantly from that region of striate cortex representing the lower left quadrant and left half field respectively. There is no similar contribution from that region on the contralateral side representing the the upper or lower quadrants of the right half field, thus full field stimulation will not result in response cancellation.

However, for subject DAJ there is a significant contribution at this electrode site from the contralateral side of the striate cortex such that when the individual responses from each quadrant are summed the comparable latency activity generated in the opposite but

Figure 9.2 and 9.3a

VEPs recorded under backward noise masking conditions for each of the three subjects studied.

The continuous trace in column A of each figure were recorded to the combined presentation of the target and mask. The dotted trace in this column are the waveforms recorded to the presentation of the noise mask alone.

In column B of each figure are shown the synthetic waveforms obtained by subtracting the mask alone waveform from the waveform produced by the combined presentation of the target and mask.

The VEP elicited by the unmasked target has been shown at the bottom of column B.

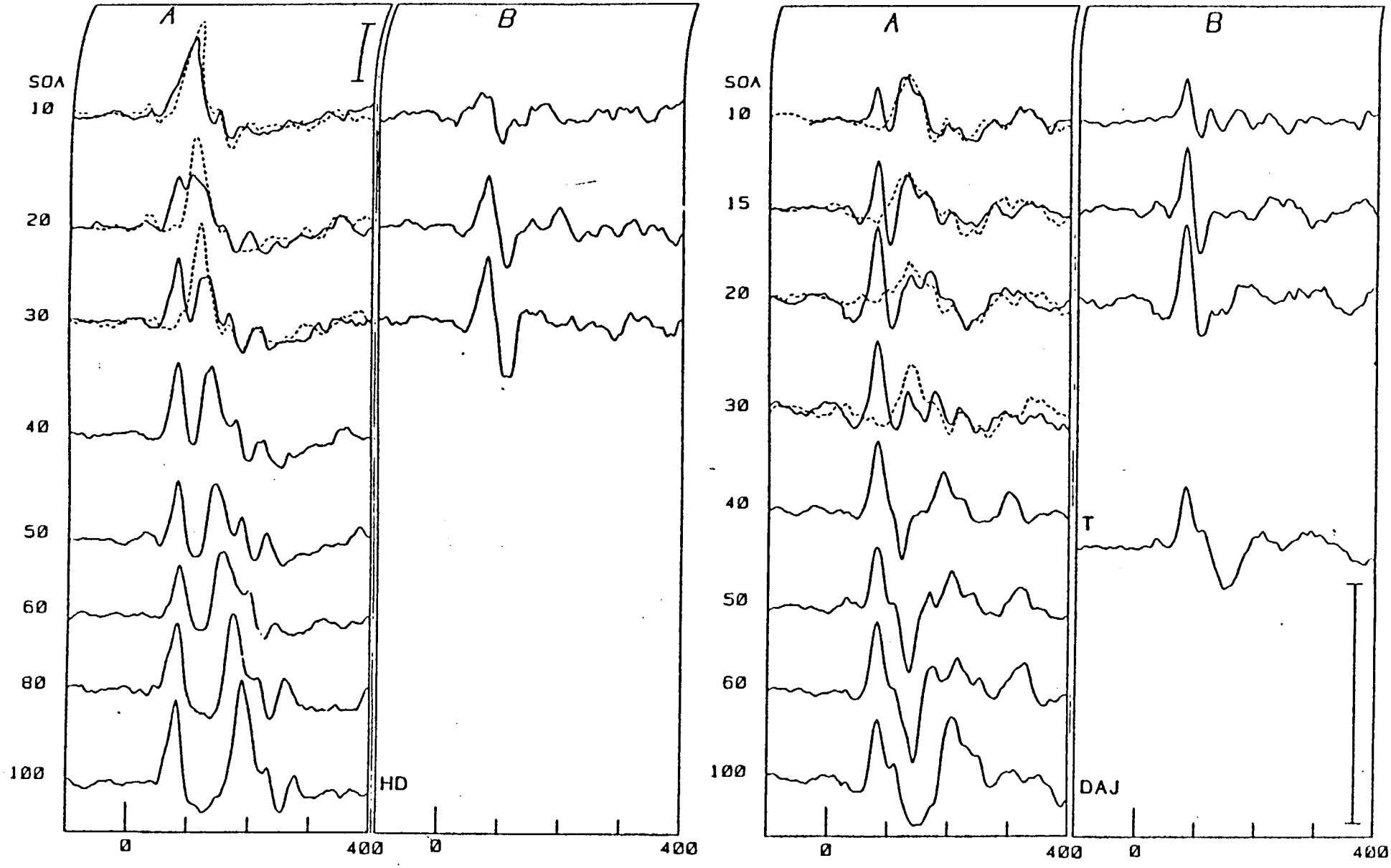
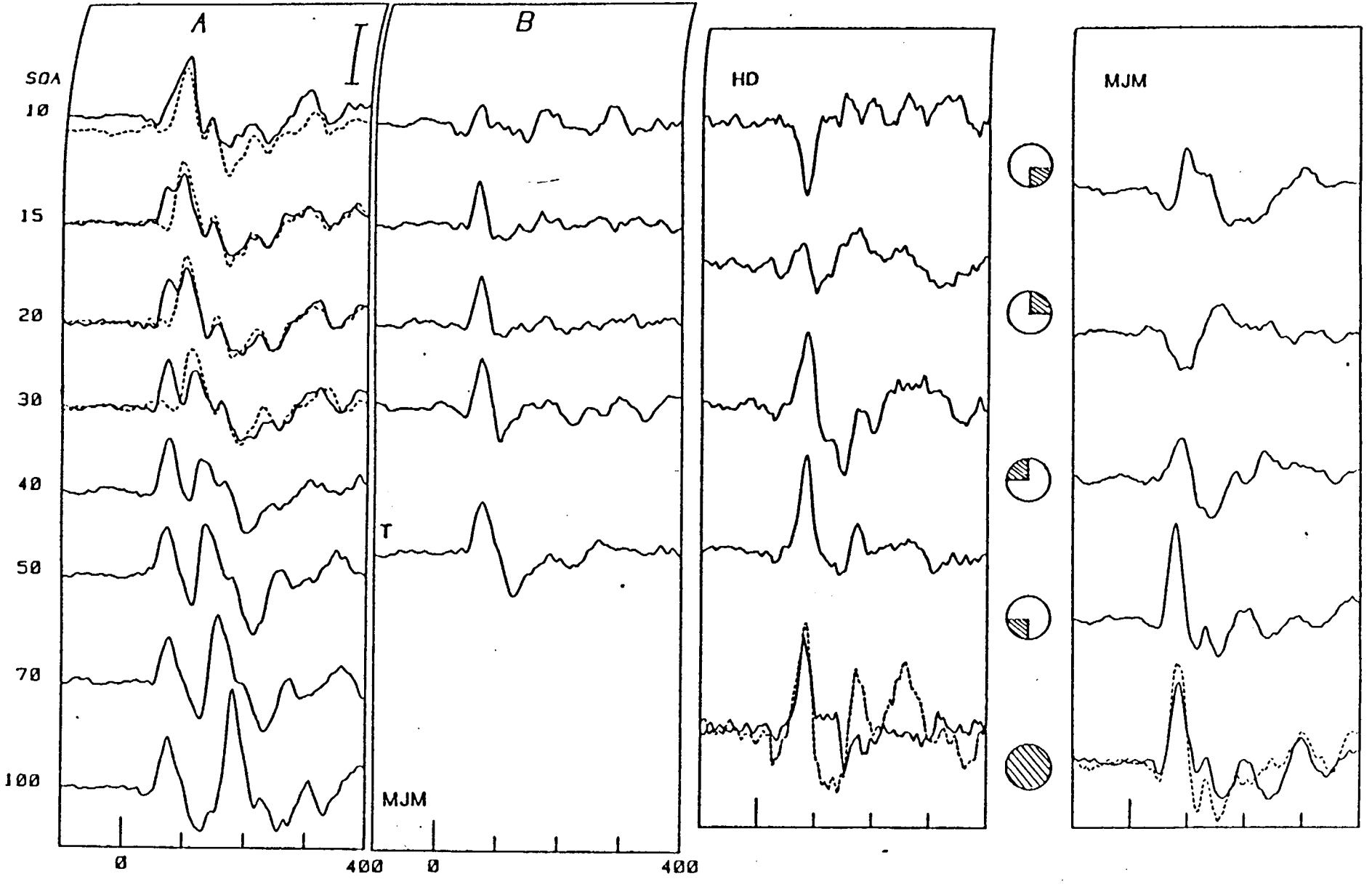

A
B
SOA
10
20
30
40
50
60
80
100
HD
0
400
0
400
A
B
SOA
10
15
20
30
40
50
60
100
T
DAJ
0
400
0
400

Figure 9.3b.

VEPs for two subjects recorded by independent stimulation of each of the four quadrants by the mask stimulus. The electrode positions are the same, and indicate that for these subjects and electrode locations major contribution to CI comes from those regions of striate cortex representing the upper and lower left quadrants.

At the bottom of each column are shown the waveforms elicited by full field stimulation (continuous trace) and the synthetic waveform obtained by computer summation of the waveforms for all four quadrants.

The VEP to full field stimulation will therefore be the sum of independent activities within those region of visual cortex representing the individual quadrants, (see text for further details).


A
B
I
SOA
10
15
20
30
40
50
70
100
T
MJM
0
400
0
400
HD
MJM

comparable regions of striate cortex will cancel. The broad positive potential seen in this subject is therefore not the response of single component but is a composite, unrepresentative of underlying physiological activity.

In figure 9.4, the target VEP amplitude (expressed as a percentage of the unmasked target VEP) has been plotted as a function of the SOA. At SOAs above above 15 msec there is no VEP attenuation, the slight attenuation of the response evident at 10 msec SOA may possible be the result of the subtraction procedure as, at this SOA, there is a large mask response for subjects HD and MJM. However subject DAJ show a similar decrease in target response amplitude which suggest that the attenuation is of physiological origin although, because of the limited temporal range of the interaction, the effect might be more logically explained in terms of retinal interactions.

9.3. Forward noise masking. Procedure.

In the following experiments a brief (50 msec noise mask) was followed by at some interval by a brief (5 msec target). The same subjects who had participated in experiment 9.1 were also used in the experiments.

Results

In figure 9.5a and 9.5b are shown for two subjects the waveforms elicited in this experiment. In each case, separate runs were undertaken with either the target or mask presented in isolation at the appropriate SOA, to allow for the subtraction of the mask response from that of the mask/target waveform, and to allow a direct comparison between the VEP elicited by the target and that of the response obtained from the subtracted waveforms.

The six separate presentations of the 5 msec target stimulus over the 1.5 hours of the experiment also gives an indication of the variability of the VEP as a function of time. To give some indication of the stability of the CI component in terms of its amplitude and latency, the six target responses have been superimposed in figure 9.6a with increased gain; also shown are the mean amplitudes of the peaks in uV. The -+ 1 SEM level is 0.172 μV the mean amplitude of the six peak is 13.6 μV. The waveform is the sum of 3 runs of 20 sweeps and clearly indicates the minimum degree of variability of these VEPs and, by

Figure 9.4

Target VEP amplitude plotted as a function of SOA for each of the three subjects. The amplitude of the response has been plotted as a percentage of the response obtained in the unmasked condition.

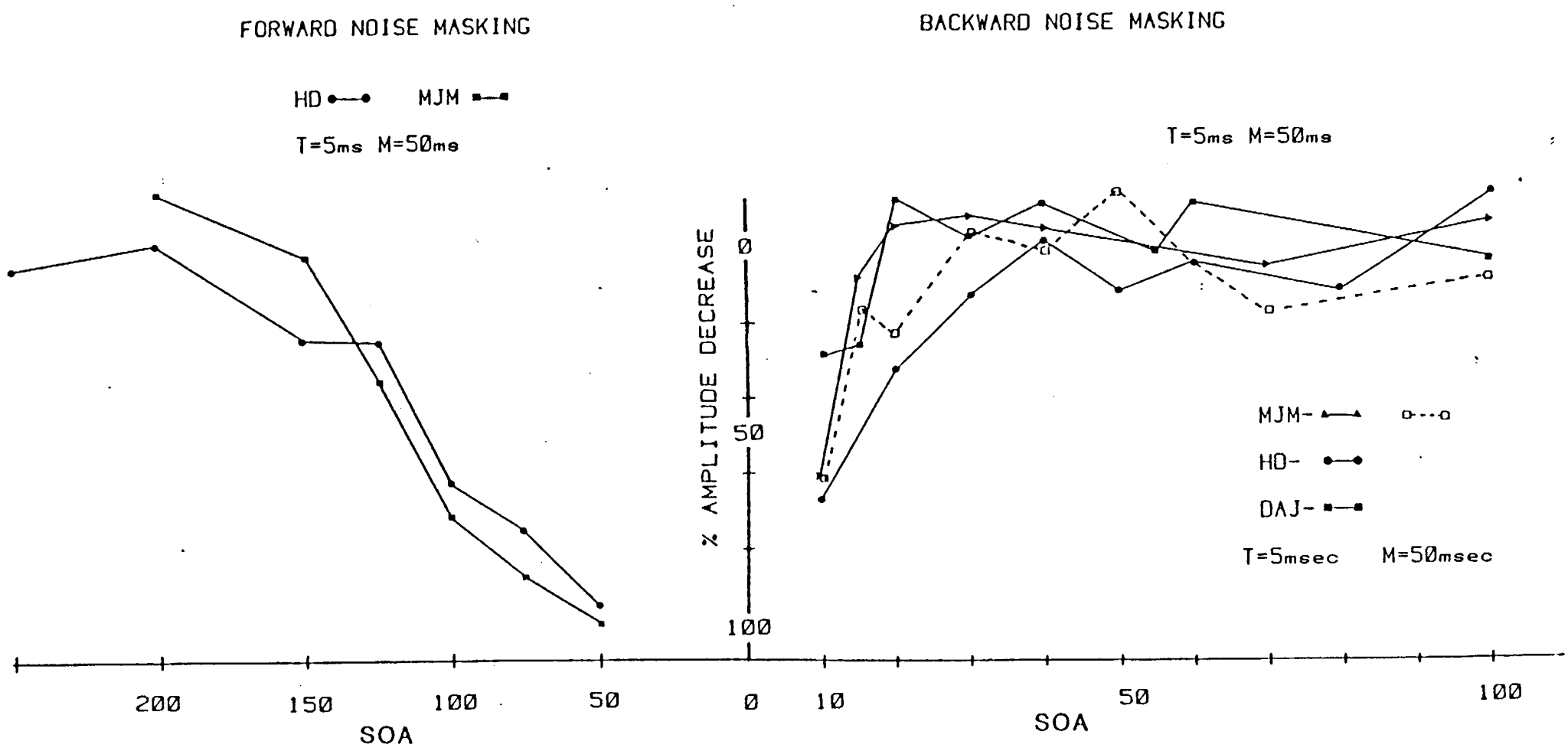


Figure 9.5

VEPs recorded under the forward masking paradigm. Fig 9.6a is for subject H.D., Fig 9.6b for subject M.J.M.

In column A of each figure are shown the VEPs obtained to the combined presentation of the mask and target (continuous trace) and mask alone (dotted trace). In column B the synthetic waveform obtained by subtracting the mask alone waveforms from the combined mask and target waveform, are shown in the dashed trace. The VEP to the target, presented in the unmasked condition is shown by the continuous trace, which for subject M.J.M. has been delayed by an appropriate onset interval. For subject H.D. target onset was held at a constant interval from the averaging trigger.

A 500 msec sample of the waveform has been shown.

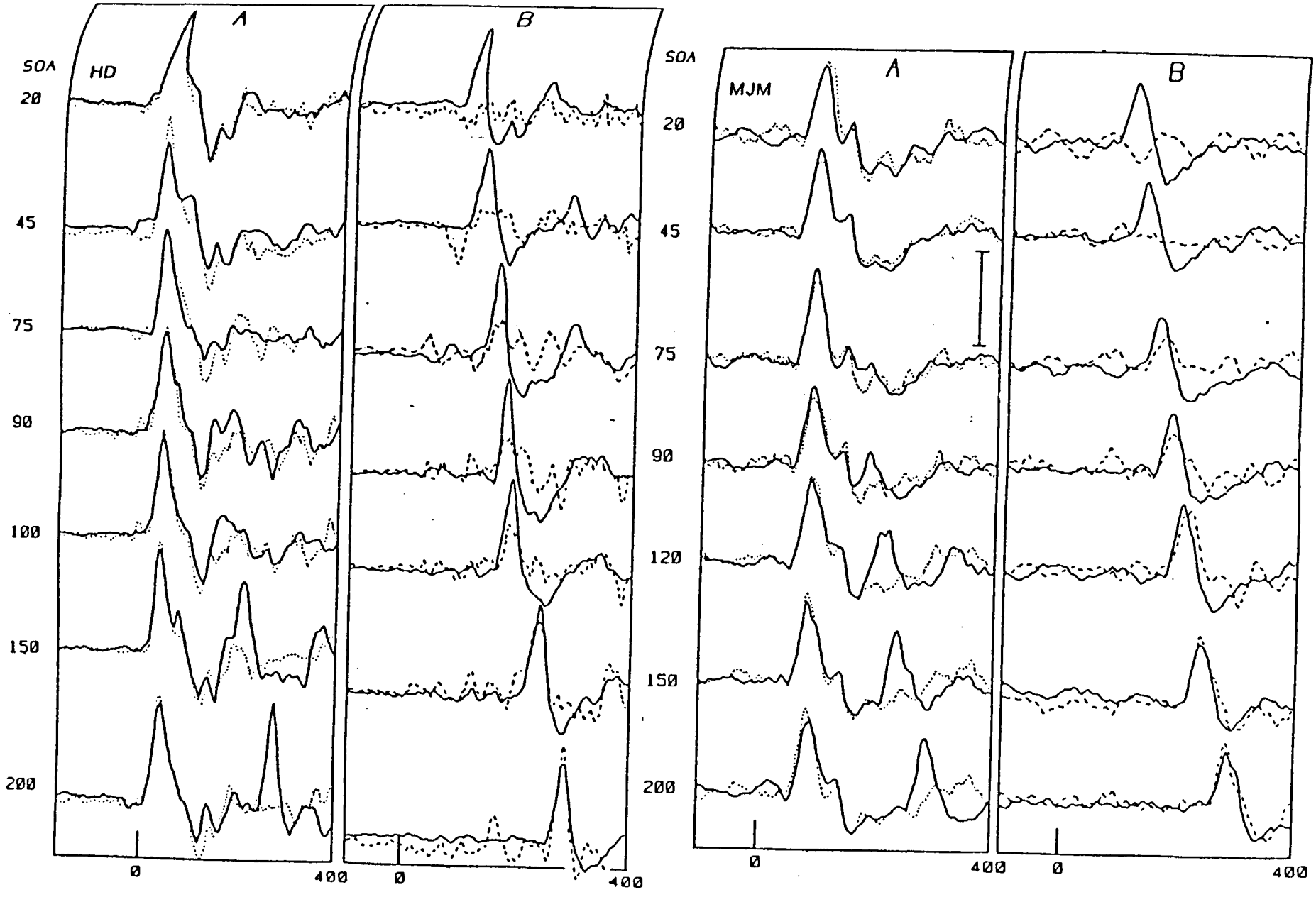

HD
A
B
SOA
20
45
75
90
100
150
200
0
400
MJM
120

Figure 9.6a

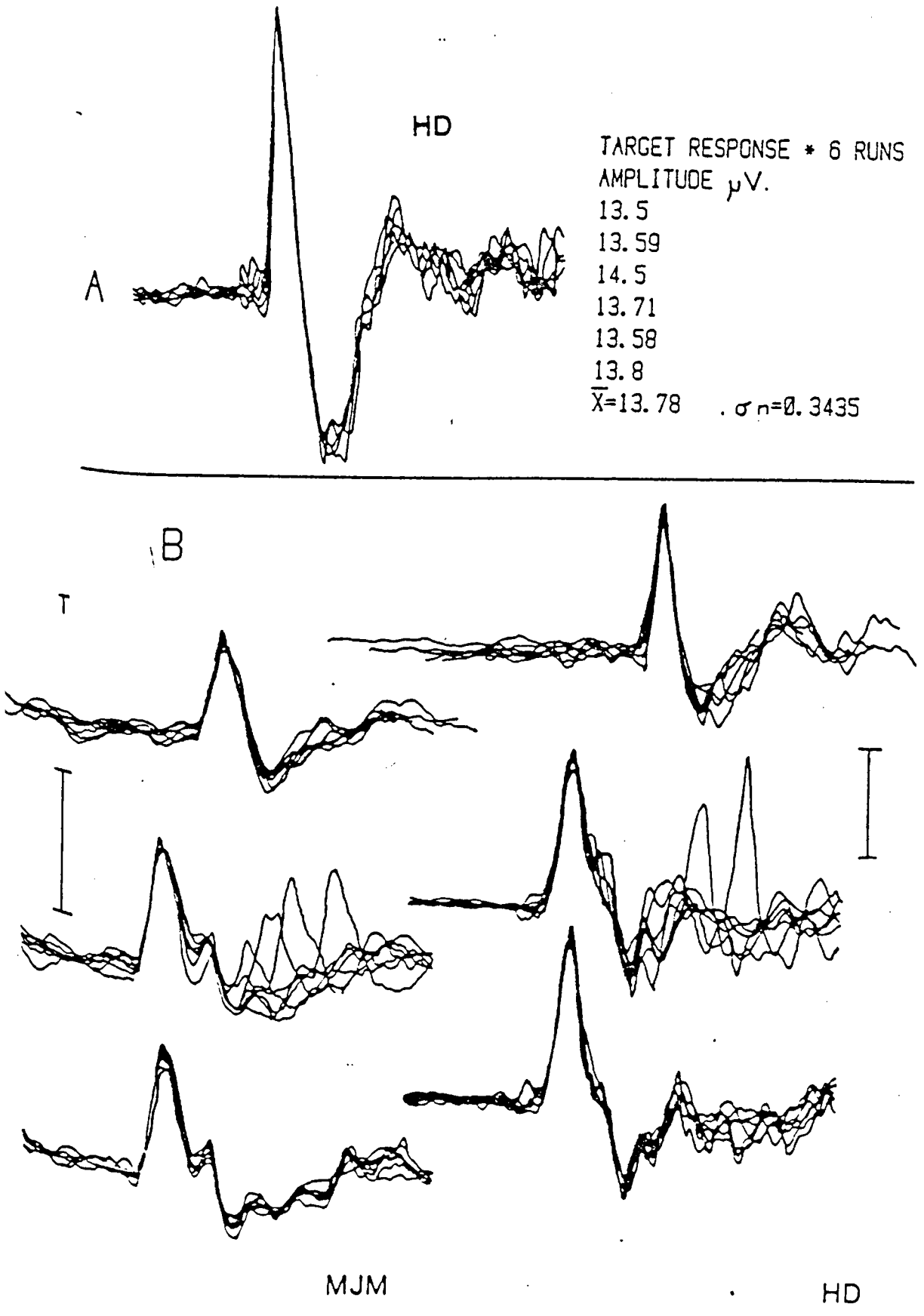
Shows the repeatability of the VEP elicited by the target stimulus in the unmasked condition. Each waveform represents the sum of 60 sweeps, and six runs have been superimposed with increased gain relative to the same waveforms shown in figure 9.6a. The mean amplitude and standard deviation of the VEPs for the six runs is also shown. The consistency of the response suggest that the cortical mechanisms within striate cortex responding to this pattern do so with a statistically invariant response.

Figure 9.6b

The waveforms shown in this figure illustrate the repeatability of the VEP recorded under the three conditions of experiment 3. The start of the waveforms elicited by the target VEP has been adjusted by the appropriate interval to be a constant temporal interval from target stimulus onset.

It is also evident from this data that in both conditions, the VEP elicited by the ~mask have a constant waveshape and amplitude. For subject M.J.M. there is evidence of a small positive peak on the trailing edge of CI which is an 'off' response.

The initial portion of the response (determined by the mask stimulus) can be superimposed exactly in the two conditions, and the amplitude of the response has a similar standard deviation to that reported for subject H.D. in figure 9.6a.


HD
A
TARGET RESPONSE * 6 RUNS
AMPLITUDE μV.
13.5
13.59
14.5
13.71
13.58
13.8
X̄=13.78 . σn=0.3435
B
T
MJM
HD

implication, the stability of the cortical mechanisms generating them. The waveforms produced by the subtraction of the 'mask alone' waveform from that of the mask+target elicited response also justified the use of subtraction procedure as it can be seen that the baseline from which the mean level prior to stimulus response was calculated is essentially flat.

The main finding of the experiment which is evident in column 2 of both figures 9.5, as well as being shown graphically in figure 9.4, is that forward masking produces pronounced target VEP attenuation. Also plotted in the latter figure is the percentage target response attenuation obtained in the backward masking experiment. The figure indicates the pronounced asymmetry of response attenuation in the two conditions.

9.4. Experiment 3:- Dichoptic noise masking

Masking effects, or indeed any psychophysical phenomena which shows interocular transfer are assumed to be mediated by cortical mechanisms (Blake & Fox,1975; Weisstein,1973) Although perhaps true to a large extent, the failure of visual phenomena to show interocular transfer does not, a priori, imply a pre-cortical locus and, similarly, the positive transfer need not necessarily preclude interactions at a pre-cortical level. It is possible that purely monocularly driven channels are preserved within the visual cortex at least up to extrastriate regions. While binocular interactions have been observed in the LGN of the cat (Sanderson,1965) and cortico-fugal fibers have been suggested to play some role in providing binocular facilitation of some LGN units (Tsmuto et al 1978; Schmielan & Singer,1977).

With these reservations in mind experiment 9.3 was conducted in an attempt to determine the extent of the interocular transfer of the forward masking interaction observed in experiment 2.

Procedure

The stimuli and presentation times were the same as for experiment 1 and 2. In the present case however, tachistoscope B was used with the mask presented to the full field of the left eye and the target the appropriate half field of the right eye.

Results

The responses are shown in figure 9.7. In column 1 for each subject are the VEPs elicited by both mask/target (full trace) and mask alone (dotted trace). In column 2 the full trace is the waveform produced by the target whilst the dotted trace is that of the subtracted response obtained by the same procedure used in experiments 1 and 2. In figure 9.7b are shown the waveforms obtained to either mask alone target alone and mask/target waveforms appropriately superimposed. The target elicited waveforms have been ajusted so that the start of each trace was the appropriate interval from the occurrence of the averaging trigger.

Once again, the figures indicate the high degree of repeatability of the waveforms over time. The main feature of these results is the significant attenuation of the target VEP observed under dichoptic presentation, the slope of the amplitude curve, shown in figure 9.8 , is monotonic for both subjects and of a similar form to that observed with binocular viewing; this suggests that the likely locus of the interaction seen in that case is indeed cortical.

9.5 Discussion

The results of these experiments have revealed a distinct asymmetry in the extent to which a subjectively powerful masking stimulus can attenuate the response of the striate cortex to a briefly present target stimulus.

In the forward masking condition there is a marked reduction in the amplitude of the CI component for SOAs up to 100 msec. The slope of the masking function being monotonic up to 200 msec for binocular viewing. A similar relationship between target response attenuation and mask onset interval was observed under dichoptic presentation, suggesting that the likely locus of the physiological interaction is within the striate cortex itself. These results support the conclusion of Wiesstein (1973) Breitmeyer & Ganz (1976) and Fox (1978) that forward masking effects are determined by neuronal interactions at relatively early stages of stimulus processing.

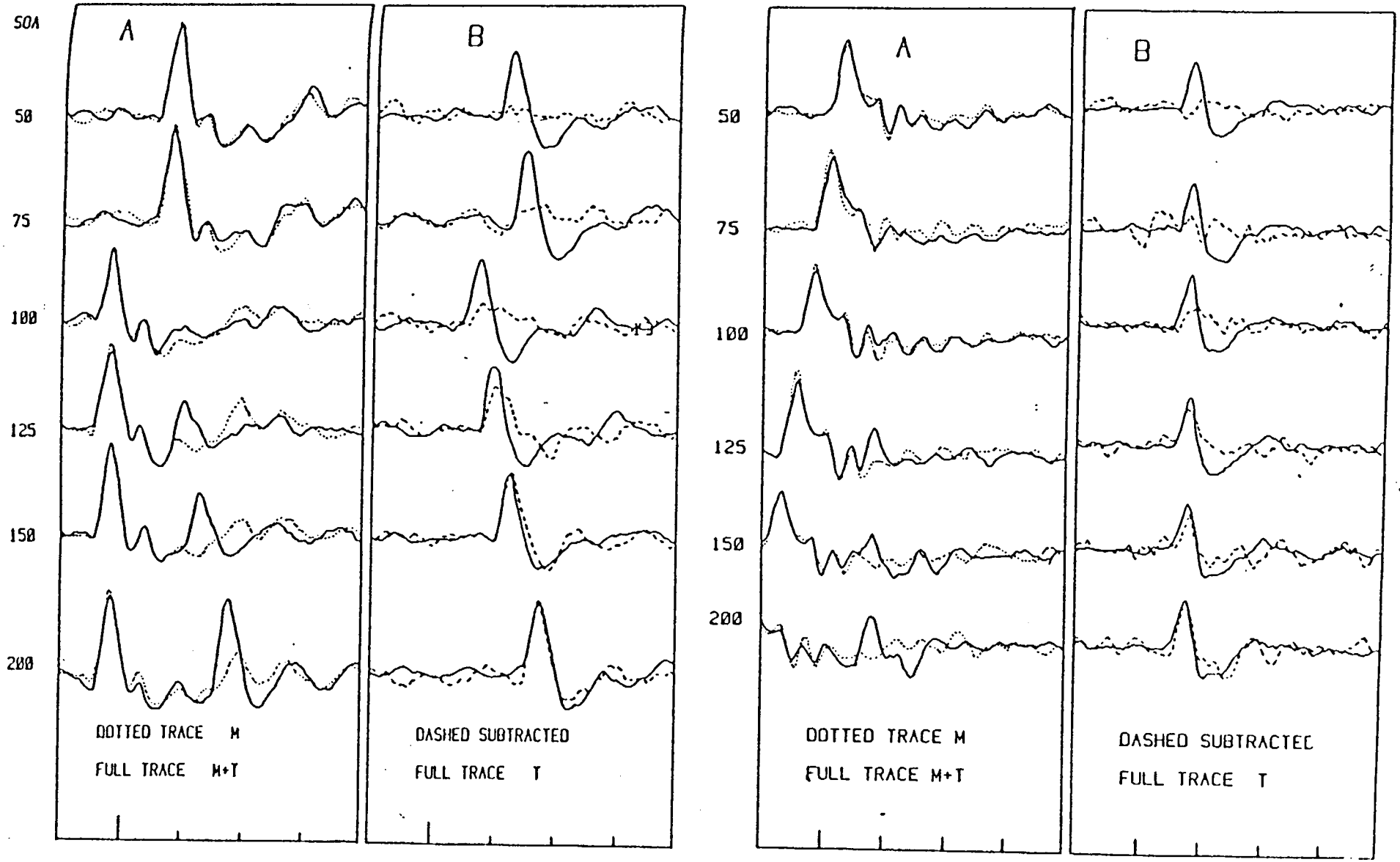
A similar conclusion has been reached by Judge et al (1980) who recorded from single units within the striate cortex of the macaque This study revealed that, for superficial layer cells driven either by a small target stimulus swept across the centre of the receptive field

Figure 9.7

VEPs for two subjects H.D. and M.J.M. obtained under dichoptic masking conditions.

In column A are shown the VEPs elicited by the combined presentation of the target and mask (continuous trace) and the mask alone (dotted trace).

In column B are shown (dashed trace) the synthetic waveforms obtained by subtracting the mask alone from the mask & target VEPs. The continuous trace in this column are the VEPs elicited by the unmasked target stimulus.


SOA
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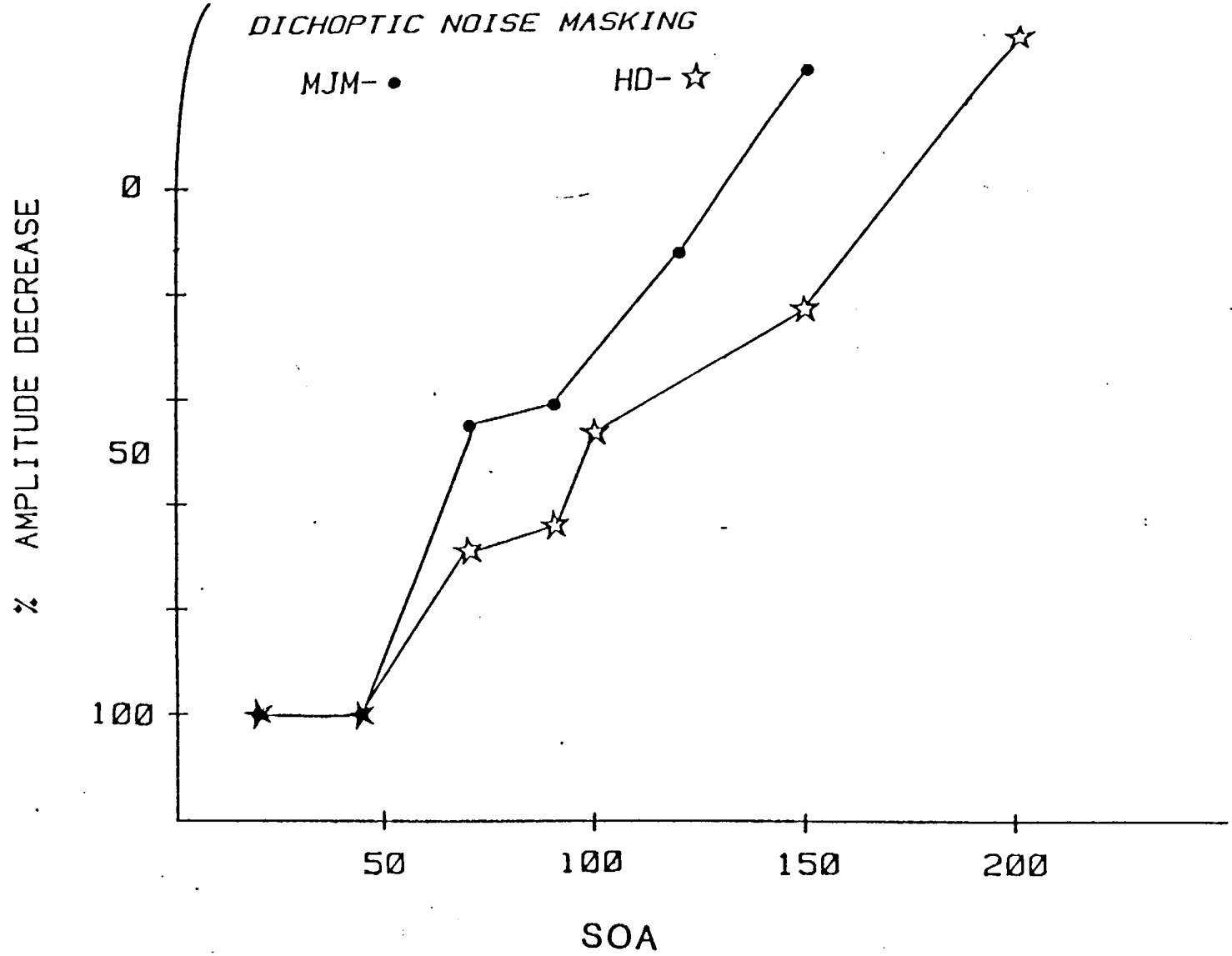


Figure 9.8

Plots of target VEP amplitude as a function of SOA under dichoptic masking conditions. Amplitude plotted as a percentage of unmasked target VEP amplitude.

at high velocity (900 cp/s) or a flash presented for a duration equivalent to the time for which the swept target would dwell on the centre of the receptive field (5 msec), pronounced response attenuation was observed when such stimuli were preceded by a flashed, masking stimulus of some 400-500 msec duration. Response attenuation was observed over a considerable range of SOAs and was, significantly, independent of the extent to which cells were responsive to the masking stimulus.

Whilst the duration of the masking stimulus used in Judge's study was far in excess of that used in these VEP experiments, and discharge amplitude plotted in terms of the ISI rather than the SOA, the slope of the masking curve (the extent of response attenuation) is similar in each case. (Indeed it should be noted that for suprathreshold stimuli with high physical contrast, long mask durations are not much more effective than shorter ones. Although Kinsbourne and Warrington (1962) have suggested that the critical masking interval, as measured by ISI or SOA, is dependent upon the mask/target subjective or physical contrast ratio)

That the interocular transfer of the forward masking interaction should be as pronounced as that found binocularly is inconsistent with the results and conclusions of both single unit (Poggio & Fisher, 1977) and VEP (Smith & Jeffreys, 1980) data which has suggested that in striate cortex of both monkey and man a very high proportion of cells are primarily monocularly driven. Poggio and Fisher report a value of 50 % for the rhesus monkey, whilst Smith & Jeffreys from comparison of the interocular transfer of checkerboard adaptation of the CI and CII components, found that CII showed almost complete attenuation whilst CI only 50 % which, they argued, was consistent with comparable single unit data from the monkey (Zeki, 1978a). However, these studies do not rule out the possibility that under certain conditions a more dynamic and short term stimulus specific inhibitory interaction may result from the brief sequential presentation of contrast patterns. The resultant effect of this interaction might be that units with a predominantly monocular excitatory drive would be susceptible to a brief inhibition mediated by cells driven by the ipsilateral eye with similar size and orientation tuning.

Some support for this suggestion comes from the demonstration by Hammond (1979) that the ocular dominance of some cortical cells in the cat are indeed stimulus dependent; the ocular dominance of complex

cells differing by three groups, on the Hubel and Wiesel ocular dominance rating scale, when tested with moving noise as opposed to moving bars. Whilst Sillito (1980) has suggested, on the basis of the excitatory connections revealed after isophoretically applying the GABA inhibitor bicuculline to specific cortical cells (GABA is a primary inhibitor), that the proportion of cells receiving some ipsilateral input is far higher than is commonly suggested on the basis of more convential tests of binocularity.

Assuming a similar organisation in monkey and man, and given the extent of the second order excitatory connections reported by Creuztfeldt (1977) and Szentagothai (1975), the strength of interocular transfer of the noise masking effects reported here, for CI, does not seem unexpected.

Backward masking

The pattern of results obtained in the backward masking condition were distinctly different from those obtained in the forward masking paradigm.

Indeed it is clear that for all but the shortest SOA (ie 10msec), the response evoked by the target stimulus remains unaffected by the presentation of the mask, although the psychophysical data shows that the target remains undetected for SOAs between 10-50 msec. Target 'detection' it should be noted is a rather low criterion response measure because the subject merely has to respond to a difference between the target/mask and the mask alone condition. Detection need not be based on the recognition of distinctive features of the target and is therefore, from the perspective of pattern recognition theories, a rather conservative estimate of the strength of one stimulus influence upon another. Despite that however, there is a distinct absence of correlation between the two measures of masking.

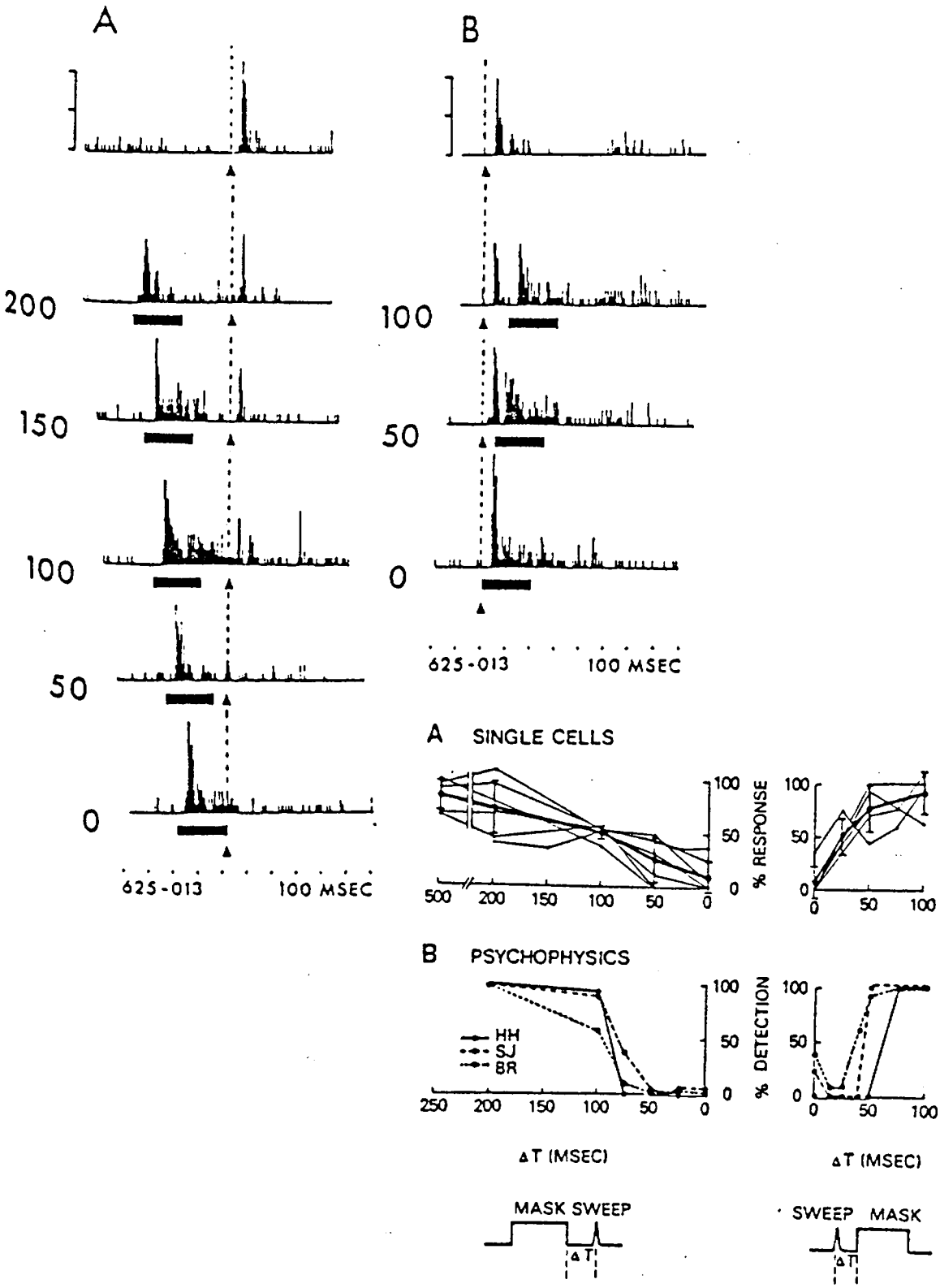
A similar lack of interaction between target and mask in backward masking paradigm was also reported by Judge et al (1980) for both sweep and flash modes of target presentation. They found that for SOAs greater than 50 msec, both target and mask responses were clearly separable (suggesting a limit of temporal resolution similar to that reported in chapter 4) with, indeed, the mask response showing evidence of attenuation as opposed to that of target. This result was not mirrored by their psychophysical data, shown in figures 9.8 and 9.9 which was equivalent to that reported here. At SOAs below 50 msec,

Figure 9.9

Taken from Judge et al (1980). Column A shows single unit discharge obtained in the forward masking condition. The onset of the 'target' is marked by the arrow head and the unmasked response is at the top of the column. The numbers at the side indicate the inter-stimulus interval. The onset and duration of the masking stimulus is represented by the contrast bar; 100 msec is indicated by the interval between dots at the bottom of each column.

Column B illustrates responses obtained in the backward masking condition. The onset of the 'target' and mask, and the duration of the latter are indicated as above. Target duration was 5 msec.

The absence of response attenuation is illustrated graphically in the inset, where percentage amplitude has been plotted as a function of SOA. The apparent response attenuation at short SOA in the backward masking condition, is as the authors point out the result of their method of response calculation, which assumes linear summation below the interval of temporal resolution (see text for detailed discussion of this point).


A
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625-013
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A SINGLE CELLS
500 200 150 100 50 0
100
50
0
% RESPONSE
100
50
0
0 50 100
B PSYCHOPHYSICS
HH
SJ
BR
250 200 150 100 50 0
100
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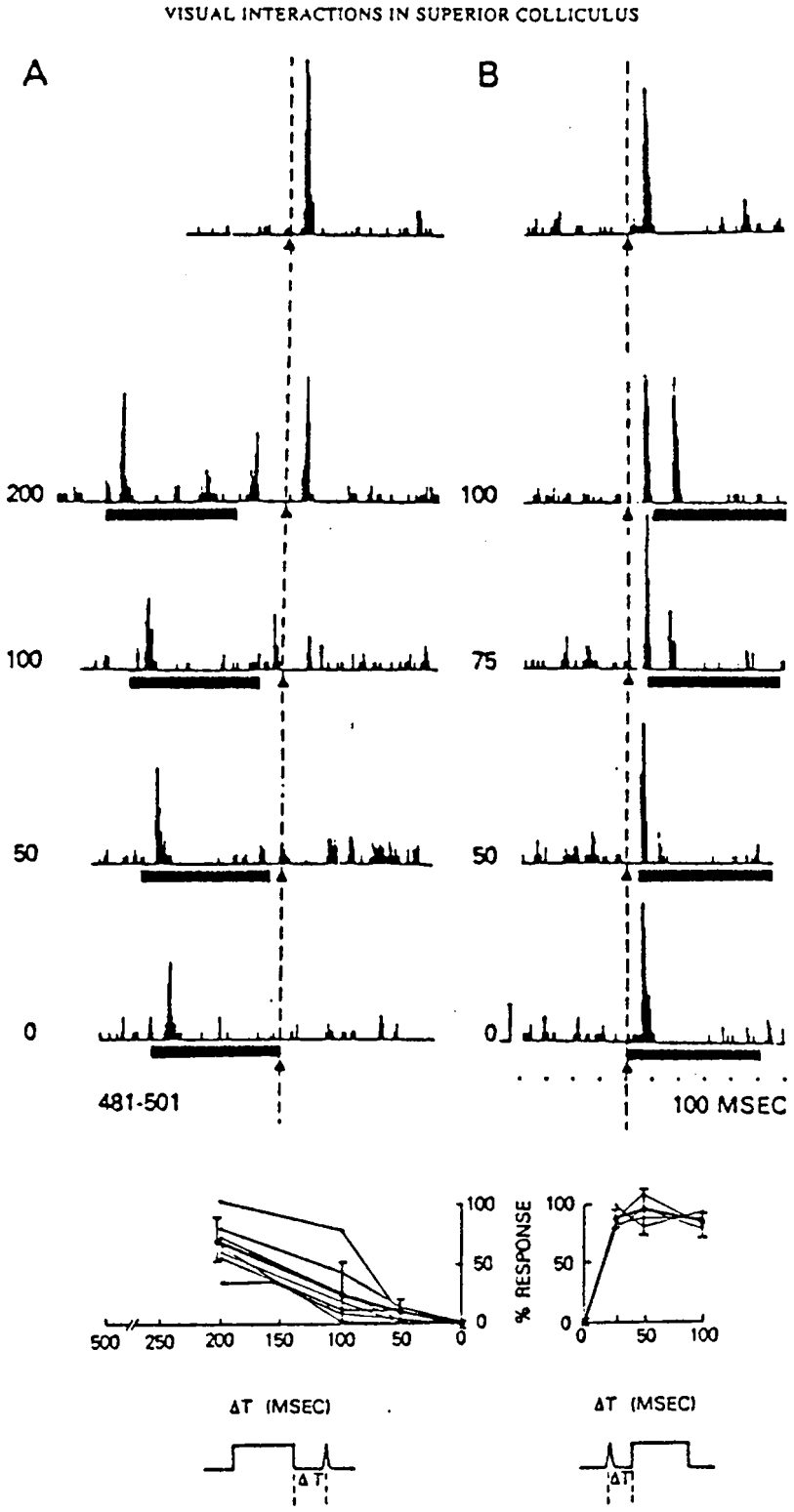


Mask Stimulus - 500 ms

Target (Flash) Stimulus - 4 ms

Figure 9.9

Taken from Richmond & Wurtz (1980).

As for figure 9.9, but in this case the responses are from units within the superior colliculus.

Judge reports that the response to the two stimuli interact non-linearly, although it is the response to the target and not that of the mask which determines the latency of discharge, even for very short SOA's. The absence of any interaction for CI is therefore entirely consistent with single unit data from the macaque's striate cortex, obtained under similar stimulus conditions. Although the VEP data is more conclusive, in that it shows a lack of interaction for a more extensive range of SOAs.

Explanations of monotonic masking functions, whether produced by noise masking or other types of spatially contiguous configurations, which have emphasized the role of response integration or processing interruption occurring at a relatively low level of visual processing, are disconfirmed by the present results. Similarly, the recent proposal by Breitmeyer & Ganz (1976), that monotonic masking functions are the result of response integration within the sustained (form or pattern processing) channels is made equally untenable, particularly in light of the fact that such integration is predicted to occur prior to, or within, the striate cortex itself.

Judge (1980) has proposed that these retroactive effects are the result of target/mask or sweep/post-sweep stimulus response confounding, and indeed the pattern of interactions that obtained at the single unit level by him would seem to support this view, since below 50 msec SOA the unit was unable to differentiate between the occurrence of the mask from that of the target, at least as evidenced by its discharge pattern. The authors argue therefore, that at the next level of processing in the chain, there would be only one 'on' response. However the "response confounding" explanation of backward masking fails to account for the fact that it is the 'mask' that is perceived rather than the target. For example, it can be shown that under the present conditions a progressive reduction in the duration of the mask significantly diminishes it's effectiveness as a masker, because of its reduced subjective contrast. When both stimuli are of the same duration (ie 5 msec) there will in fact be no subjective masking. The response confounding explanation would predict that under these conditions the latency of the cortical activity elicited by the mask would be significantly longer, concurrent with the increased detectability of the target. However it has been shown in chapter 3 that the latency of cortical activity as measured by the CI component is independent of stimulus duration, and therefore of subjective contrast. A similar effect has been reported at the single unit level

(Levick & Zacks,1970; Baker et al,1969; Galletti,1979).

Defining a stimulus as a mask is an operational procedure based on it's effectiveness in reducing the detectability of a preceding or succeeding stimulus. Accordingly, Judge et al's account of retroactive masking, can give no explanation as to how an operationally defined 'mask' does not become a target. [It should perhaps be noted that his own data contain the seeds from which doubt can be cast on the validity of the response confounding explanation of masking. Specifically, they note in their discussion that for forward interactions, the response of many units to the target showed an equal amount of attenuation irrespective of whether the masking stimulus had in fact provided excitatory drive (see above). Now, when the target precedes the mask these same units will respond to the former but should show no response to the latter, therefore, there will be only 'one' on response which will be unconfounded. As the authors provide no explanation as to why it is that those units that are claimed to show discharge interaction should be more important for target detection than those which do not, the theory must be considered unproven].

If the preceding analysis is correct, then at the next level of processing, presumably the extrastriate visual areas which are known to receive afferent projections from striate cortex (Zeki,1978a,b), it should be possible to observe two distinct peaks of activity, each of which is time locked to the presentation of either the target or mask. In the following section of this chapter an attempt was made to do exactly that, by simultaneously recording the isolated CI and CII components elicited by both target and mask stimuli.

In summary, the data reported here for CI are entirely consistent with the responses observed at the single unit level within that region of visual cortex predicted to be its source locus. The results provide evidence to the effect that monotonic forward masking functions obtained with equal intensity stimuli may result from brief inhibitory interactions within the striate cortex. A type of interaction somewhat different from the notion of response integration.

9.6. Backward noise masking:- CII

The question under debate, therefore, is whether there is any interaction between, the striate cortex and those areas of extrastriate

cortex which receives direct input from it, which may correlate with subjective masking.

Now the model of Jeffreys & Axford (1972) proposes that the generator of CII lies somewhere within extrastriate cortex and further, that it's properties are such as to suggest that it receives direct input from that region of cortex generating CI (see Jeffreys, 1977). Ideally therefore, to answer this question one would have to simultaineously record from both components the activity evoked by 'both' stimuli to assess the possible inhibitory effect of the mask at levels succeeding the of striate cortex. This is a difficult procedure, because pattern specific components, give rise to temporally overlapping responses and, unless conditions are chosen which optimally isolate the relative contributions of these underlying activities to the signals recorded at the scalp, one is not justified in attributing specific properties to the underlying generators.

However, for some subjects and under some conditions, the use of a particular electrode array and an area of retinal stimulation can give rise to the simultaneous isolation of both CI and CII as shown below.

Experiment 9.4:- Procedure.

The stimuli were similar in form and duration to those used in experiment 1,2 and 3. Bipolar electrodes, 5 cm either side of the midline 4cm up from the inion were used to record CI. Whilst an active midline electrode 4cm up from the inion with reference to the right ear was used to record the CII component.

The experiment was divided into two parts. The target was presented to the left half-field in part 1 and to the upper half-field in part 2; the mask was presented to the full field in each case.

In the following experiment, runs consisting of both target and mask, and mask stimulus alone were undertaken at each of the randomly determined SOA values ranging from 10-70 msec, in 10 msec steps, which allowed, where necessary, the subtraction of the VEP to the mask form that of the VEP evoked by target and mask.

Results

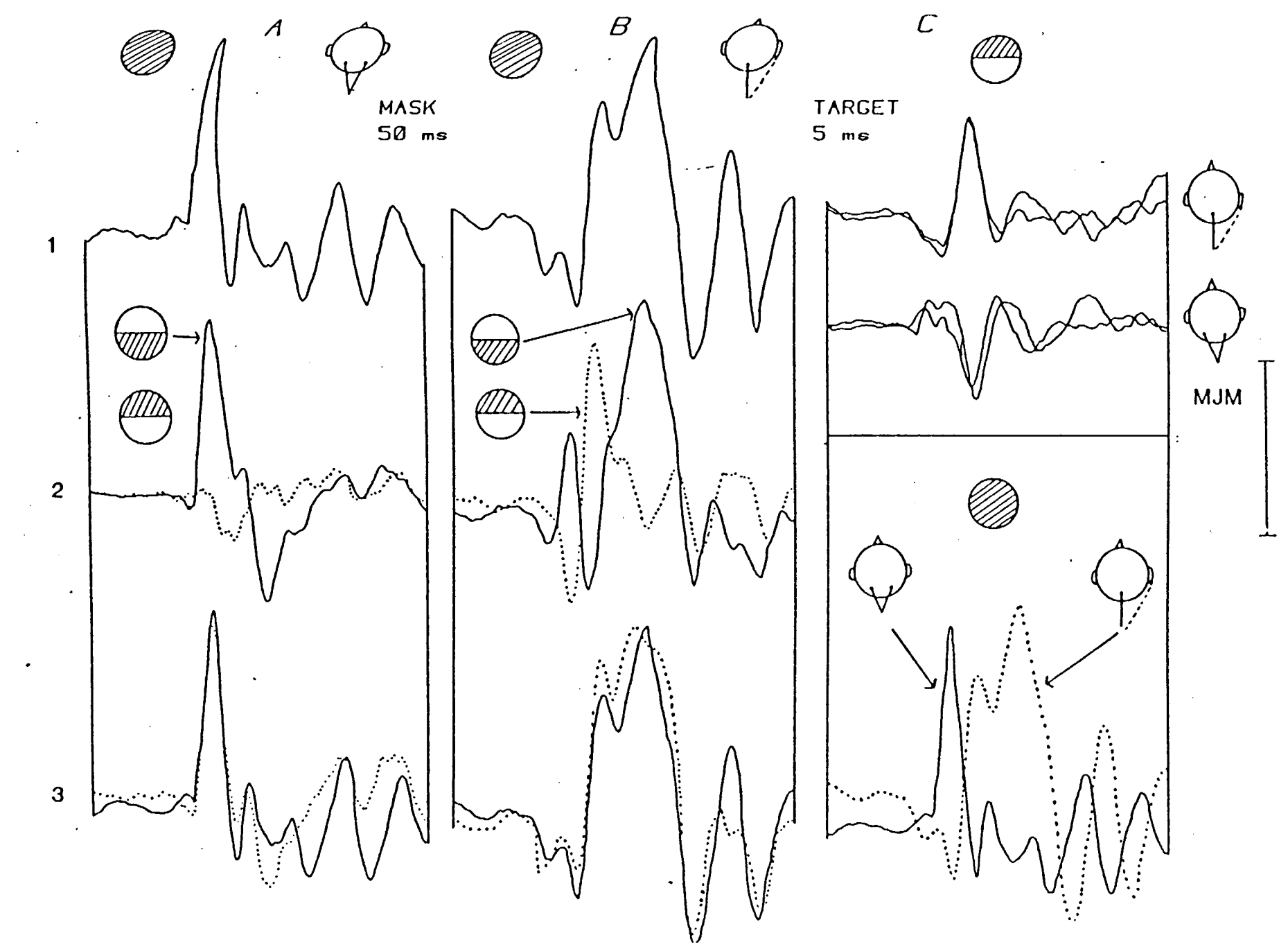
To justify the rationale behind these experiments and to give some indication of the nature and composition of the waveforms which are

Figure 9.10

Shows the composition of the VEPs elicited by full and half-field mask stimuli from the two electrode derivations used in the following experiments.

Column A:- VEPs elicited by the noise mask with bipolar electrodes 5cm each side of midline.

Column B:- VEPs elicited by the noise mask with monopolar midline electrodes used to record CII.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TARGET
5 ms
MJM
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2
3

illustrated in the following figures, I have shown in figure 9.10 the typical form of the response obtained to upper, lower or full field stimulation from the present electrode positions. Also shown are the waveforms obtained when the responses from independent stimulation of these regions have been summed.

In column A are shown waveforms for the bipolar electrode derivation. The full field mask produces a large positive potential which, as seen from a comparison with the waveform in row 2, is apparently produced almost entirely by activity in that region of striate cortex representing the lower half field. (in reality this activity is generated entirely in that region of striate cortex which represents the lower left quadrant). Summed, the VEPs to upper and lower field stimulation produce, exactly, the full field elicited waveform.

In column B are illustrated the responses recorded at the midline electrode, to independent upper and lower field stimulation. The waveform here is of greater complexity as activity of all three components (CI,CII and CIII) can be identified. The peaks reflecting the activity of these three components clearly reverse polarity as a function of upper and lower field stimulation and should therefore produce potential cancellation with full field stimulation. However under such conditions there is only partial cancellation because of the differential amplitude of upper and lower half field VEPs.

The peaks reflecting CII and CIII for upper and lower field cortical representations interact to form a broad positive potential, a composite, which is replicated by summing the individual responses for the two appropriate half fields, as is shown in row 3 of column B.

Shown in row 1 of column C are the waveforms for both electrode derivations used in this experiment, obtained in response to the upper field target. At the shorter stimulus duration the midline electrode shows a single postive peak at about 105 msec, which is the CII response. It is preceded by a small negative potential which is CI, as shown in column B to the longer duration and hence more potent mask stimulus. With the bipolar electrode placements used to record CI, a small negative potential is produced at about the same latency as CII. However further study was not undertaken to determine whether in fact this was CII.

In row 3 of column C are shown the VEPs elicited by the mask stimulus and recorded from both the monopolar midline and the bipolar electrodes. This figure illustrates the importance of component isolation with regard to any detailed examination of pattern specific potentials, and questions the dubious principle of attributing specific properties to individual peaks ofl waveforms recorded from a limited electrode array. The VEP from the midline electrode is in fact similar in form to that reported by both Schiller & Chorover (1967) and Vaughan & Silverstein (1969), who also used full field stimulation in their studies of masking phenomena. The broad positive potential similar in form to that which has been attributed by some to reflect some long-lasting cortical response is, as was shown in figure 9.10, a composite. However, the significant point is that the large positive potential obtained from the bipolar electrode is little evident in the waveform obtained at the midline and would have been overlooked had not this electrode placement been utilised.

Results and dicussion

Having discussed and justified the rationale behind these experiments, I will now consider the results from the masking experiment itself.

Figure 9.11 shows the waveforms obtained from the midline electrode to the upper half field target followed by the full field masking stimulus. The full trace shows the target and mask response and the dotted line the mask alone response. The arrow above each trace indicates CII target response. There is little attenuation of the CII component elicited by the target stimulus; as can be seen for SOAs of 20 msec and above, there is a clear and well defined peak, which has a constant latency of 105 msec. The lack of attenuation of CII is clearer from a comparison of the subtracted responses shown in column B. At SOAs of 20-40, msec the slight decrease in amplitude of the target VEP evident in the unsubtracted waveform is clearly the result of the temporal overlap of this peak with the small negative potential preceding the larger positive peak (the broad composite discussed above) which is seen in the 'mask alone' waveforms (dotted trace).

In summary, the evidence does not support either the response attenuation or the response confounding explanation of retroactive pattern masking, at least as proposed in their current forms.

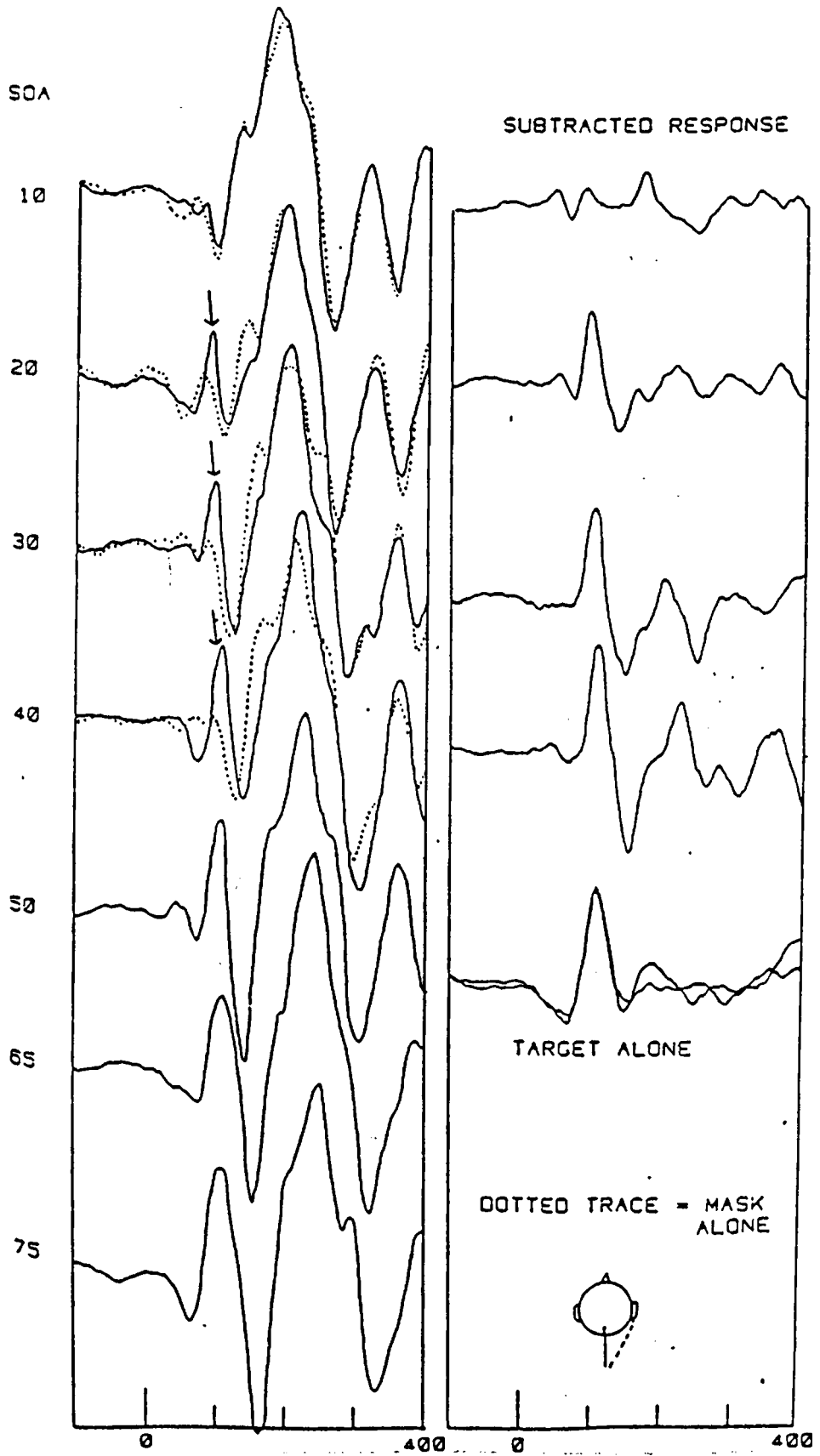
Figure 9.11

Waveforms obtained from the midline electrode under masking conditions.

In column 1 the continuous trace was recorded to the combined presentation of the upper field target and the full field noise mask. CII is arrowed at short SOAs.

The dotted trace in this column was obtained by the presentation of the mask in the absence of the target. In column 2 are shown the synthetic waveforms obtained by the subtraction procedure outlined in previous sections.

At the bottom of this column are shown two runs with the target stimulus presented alone to indicate the repeatability of these VEPs elicited by these stimuli of low subjective contrast.



9.7. Possible electrophysiological correlates of noise masking

A theoretical stance taken by many workers in the field, is to quote Barlow (1969), that

> "a description of the activity of a single nerve cell .... is a complete enough description for the functional understanding of the nervous system ..... the firing of a given nerve corresponds to a high degree confidence that the precept is present in the external world".

The evidence reviewed in the introduction should be adequate to prove that such a simplified notion of the relationship between single cell activity and "perception" is radically misplaced with regard to the processing of more complex visual stimuli. The former may be a necessary condition for the latter, but it is not a sufficient one.

There is indeed much evidence indicating a close relationship between single unit and VEP properties, and subjective sensation, particularly in the domain of subjective and physical contrast, as already shown in this thesis. Yet we are still a very long way from achieving any understanding of the neural processes that allow the integration of information over the whole field to form a unified and stable picture of the visual world.

The major afferent pathways from the retino-cortical system have been studied in some detail and figure 1.5 gives some idea of the complexity of those major connections within the visual cortex itself. However very little is understood about the properties of cells within those regions succeeding V1 (though see Zeki (1978a,b,c,d), and chapter 1). In view of the limited information available it becomes an indictment of many psychophysical theories that visual phenomena are modelled solely in terms of receptive field properties of cells observed within the retino-striate system. The neural representation of any visual stimulus does not begin and end with activity within the striate cortex.

The distribution of processing within the visual cortex, in terms of the cardinal statistical properties of a stimulus (colour, motion, relative position on the retina) is a distribution not only in space, but in time, as by the very nature of the serial afferent input to these cortical regions it must be. The debate as to whether serial or parallel processing is undertaken at cortical level has always been of questionable importance: both types of processing are undertaken, (see for example Hammond & MacKay (1977) and Creutzfeldt (1981).

In visual tasks such as reading, fixations commonly lasts between 150-200 msec between which are dispersed saccades and other less violent eye movements, the former of which take between some 25-100 msec to complete, depending on size. Jeffreys (1980) has shown that the pattern-onset VEPs studied in this thesis can be evoked by saccadic eye movements from a patternless area (equivalent to the blank field used in the tachitoscope method of stimulus presentation) to a patterned field. The distribution and properties of the potentials thus evoked were similar to those obtained with the tachistoscopic presentation such that, for example, prior fixation of a pattern similar to that onto which the subject made the saccadic movement causes substantial attenuation of the response evoked by the saccadic stimulus itself.

Figure 9.12 illustrates the VEP analogue of the temporal dispersion of visual stimulus representation discussed above. However this case are also illustrated the consequent temporal overlap of neuronal excitation resulting from the rapid sequential presentation of both target and mask.The VEP, arrowed and shown in the full trace, is the CI component evoked by the target and recorded with bipolar electrodes to left half-field stimulation. The VEP in the dotted trace is CII to the target presented to the upper half field; the first three waveforms were obtained by subtraction of the target/mask waveform from the mask alone waveform; again only the first 250 msec of the waveform has been shown. The large VEP shown in the full trace, but not arrowed, is evoked by the full field mask stimulus, recorded from the bipolar electrode, with the target confined to the upper half field. For SOAs between 10-40 msec two or three separate runs have been superimposed to give some indication of the repeatability of the response.

At SOAs of 10 msec both CI & CII evoked by the target are attenuated, the latter to a greater extent than the former. Beyond this onset interval neither component shows response attenuation. CI is always temporally separate from that of the response to the masking stimulus as was shown above. This is not the case, however, for CII, which for all SOAs up to 50 msec, is completely or partially contiguous with the response of the striate cortex to the masking stimulus. The significant point is that it is exactly at the point at which CII is no longer temporally contiguous with activity in striate cortex, as indicated by CI to the mask, that the detectability of the target as measured psychophysically increases, from below chance to approximately 70-100 %.

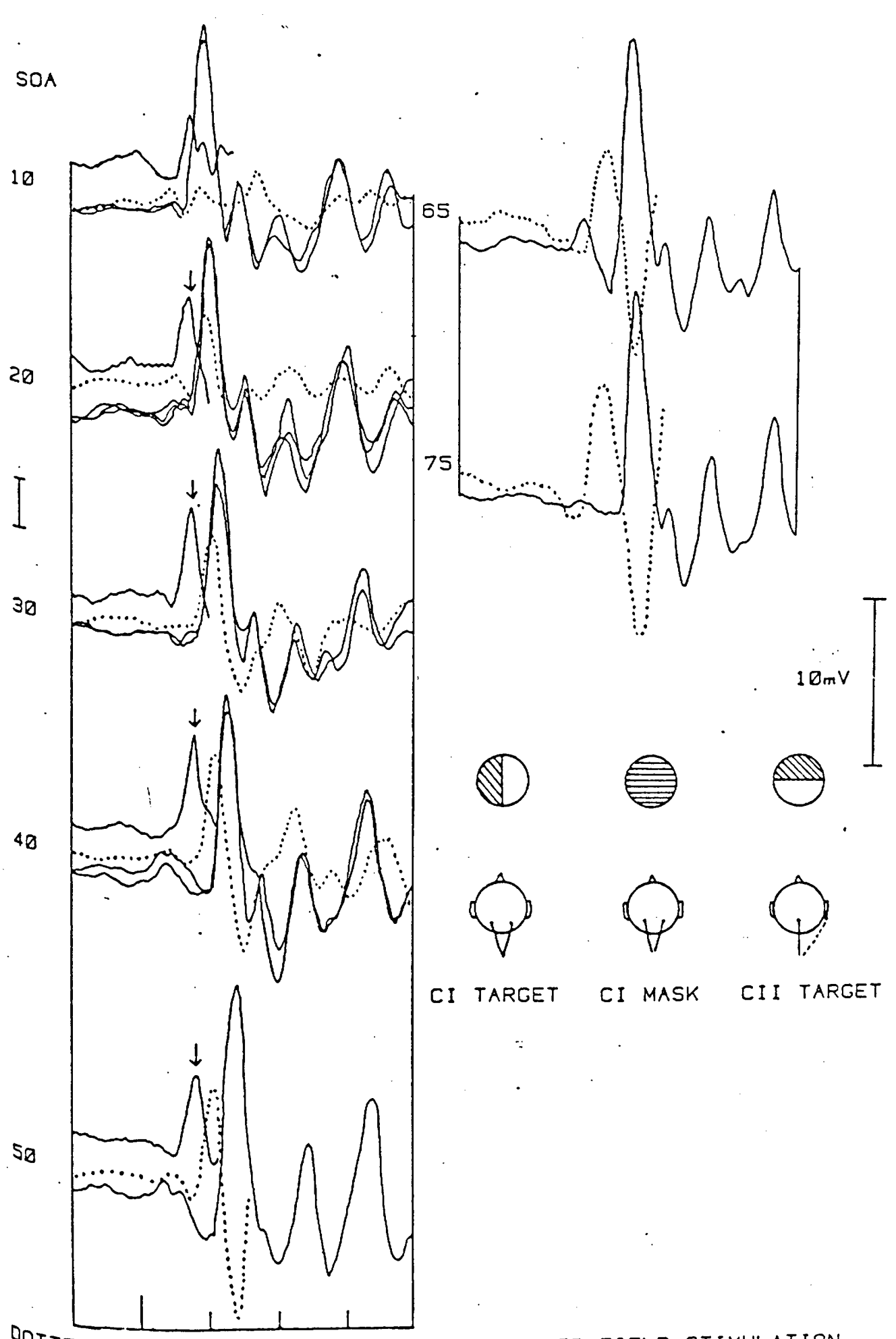
Figure 9.12

The time course of activity at the site of the CI and CII generators as a function of the temporal interval between target and noise mask.

The VEP shown in the dotted trace are CII elicited by the target presented to the upper half-field with a full field mask. For traces from 10-40 msec SOA the waveforms have been obtained by the subtraction procedure, and are shown in column 2 (these waveforms are recorded from the midline electrode).

The arrowed, continuous trace, is CI recorded from bipolar electrodes to the target presented to the left half field. These repesent the sum of 5 one trial sweeps (see figure 9.15), only 250 msec of the sample have been shown. The appropriate 10uv calibration bar is shown to the left of the figure.

The second continuous trace, of which a 500 msec sample has been shown, is CI elicited by the full-field mask recorded from the bipolar electrodes simultanious with the recording of CII to the upper half-field target (see figure 9.12). In some cases (at SOAs between 10-40 msec) two or more runs have been superimposed to indicate the repeatability of these VEPs (see text for detailed discussion).



DOTTED TRACE = CII TARGET RESPONSE UPPER FIELD STIMULATION
ARROWED TRACE = CI TARGET RESPONSE LEFT " " " "
LARGE TRACE = CI MASK RESPONSE FULL " " " "

Although possibly coincidental, the above evidence suggest that one possible factor determining retroactive masking phenomena is the limited ability of the system to correlate the temporally dispersed neural representation of the stimulus when succeeded at some short interval by activity evoked by a later, more potent stimulus.

If a visual stimulus is represented by spatially and temporally distributed activity within those functionally distinct regions of visual cortex, the VEP data would suggest that the brief presentation of a contrast stimulus produces a sequence of neural activity which last, for some 250 msec, since the overall time course of the CI, CII and CIII components is equivalent to this value (see Jeffreys and Musselwhite, in prep). This is a rather extended period compared to the time course of subjective masking reported here although, as I have noted, the psychophysical detection criteria was rather low. If the presentation of a brief patterned stimulus produces this pattern of temporal activity then the subsquent presentation of the masker may disrupt processing, involving not only activity within striate-extrastriate pathways but also activity in pathways which feedback to striate areas from extrastriate cortex. Van Essen & Zeki (1978) have shown that V2 has a direct projection from striate cortex but in turn sends fibers back to V1.

The dispersion of information within visual cortex, as suggested by for example Zeki (1978a,b,c,d) and must allow for a high degree of specialised information extraction. However this spatial (cortical) dispersion of information is, as a principle of information processing, not without limitations, the information has, after all, to be correlated at some point; a process which in turn dictates some form of fine temporal tuning which might be disrupted by this unnatural form of stimulation. The recognition, or indeed detection, of visual patterned stimuli may depend upon the uninterrupted completion of neural processing within all retinotopically organised regions of visual cortex. The apparent limitations on the temporal processing of brief, partially sequential stimuli need not have any simple neural correlate, as suggested by the present VEP data, but may reflect limitations in processing at a more 'global' level.

The masking phenomena studied in this chapter will perhaps only be adequately explained when we have a clearer understanding of the way in which visual stimuli are represented within the cortex at a global level.

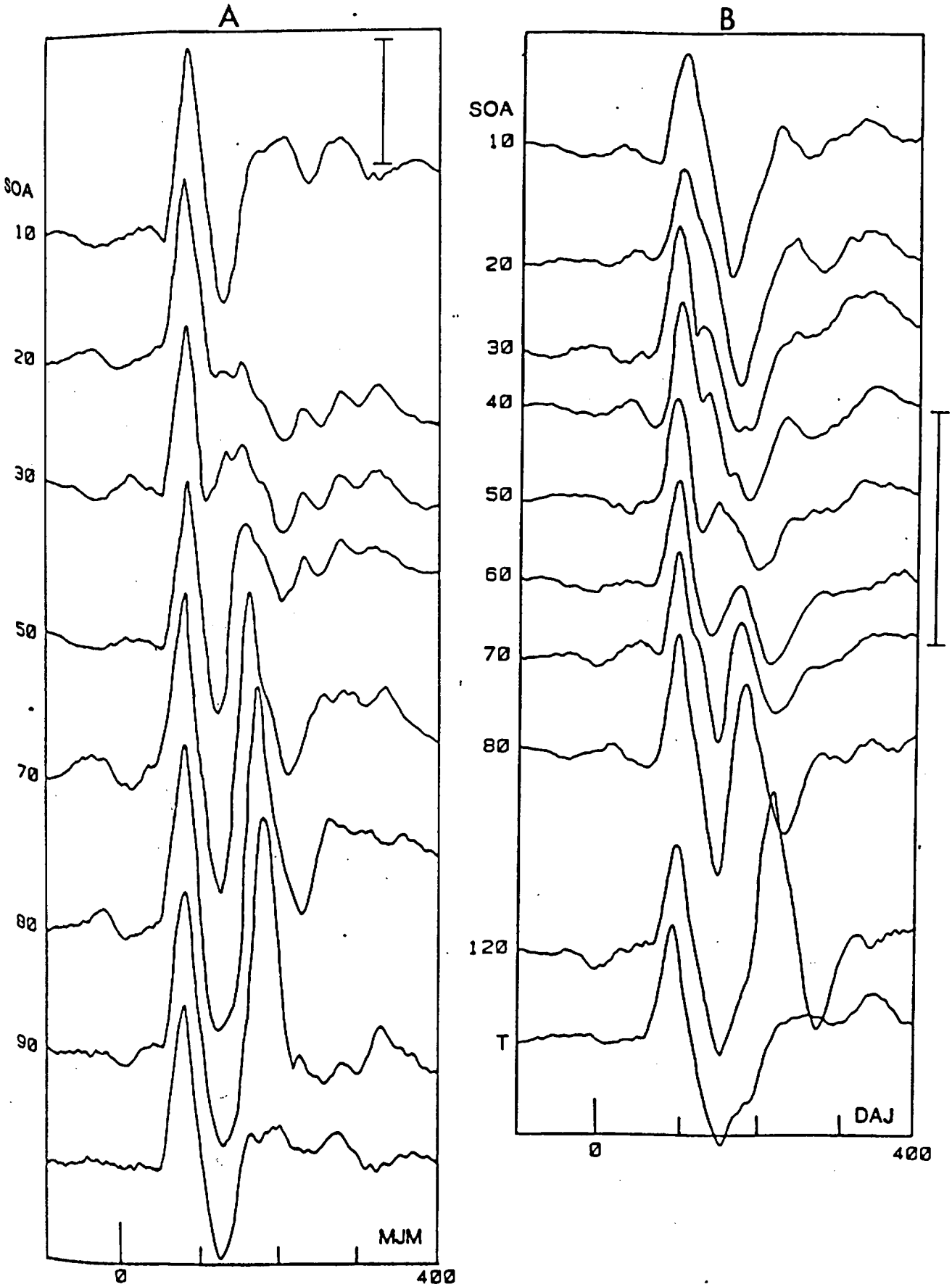


Figure 9-13

Column A:- VEP elicited by a checkerboard target of 5 msec duration and a checkerboard mask of 100 msec duration. The check width of both stimuli was 10.5'arc and they were positioned 180° out of phase. Under these conditions the target is undetected up to SOA's of 80 msec.

Column B:- VEPs elicited by a square wave grating target of 5cpd presented for 3 msec followed by a 100 msec masking grating of 3cpd.

The experiments so far reported above have concentrated on masking by patterns of visual noise; however, other types of masking stimuli, such as gratings and checkerboard, were also used. In figure 9.14 are shown waveforms from two typical cases. In both case the target presented at twice the duration threshold was completely masked for SOAs up to 70-100 msec. As can be clearly seen there is no attenuation of the VEP elicited by the target over the range of SOAs for which subjective masking is complete.

Chapter 10:- Adaptation studies.

Introduction

Psychophysical studies have revealed two important adaptation phenomena; namely, the contrast elevation effect (Campbell & Blakemore,1969; Pantle & Sekular,1968) and the frequency shift effect (Blakemore & Sutton,1969; Blakemore,1970). While these effects may have tapped mechanisms which underlie the more classic visual illusions (Ginsburg,1973), they have added the much needed dimension of 'measurement', e.g. frequency shift or percentage threshold elevation, which has enabled a more exact quantification of the extent and range over which various types of stimuli disturb the underlying physiological mechanisms on which our visual perception of the world is presumably based.

Specifically, such experiments have shown that prolonged inspection of high contrast square or sine wave of frequency f_a, will cause a pronounced elevation of the contrast threshold of test gratings, with a frequency f_t, the maximal elevation occuring when $f_t=f_a$, (see Braddick et al, (1978), for a review).

The robust nature of the adaptation phenomena associated with gratings and other such stimuli of simple periodic contrast profile, led Campbell & Robson (1968) and others to propose that spatial frequency tuned contrast elevation effects and frequency shift phenomena are of themselves evidence of frequency coding within the visual system based on a Fourier analysis of either the whole of the visual field (Ginsberg,1971) or on a piece wise analysis of isolated patches of it which are then synthesised at some later stage of processing (Glezer,1973; Robson,1976; Pollen & Lee,1971; Maffei & Fiorentini,1973;).

Many studies have been conducted in the search for neurophysiological correlates of these postulated Fourier analysers, one of the most extensive, and detailed, being that of Andrews & Pollen (1979). They suggest that cortical cells perform a 'strip integration' over a limited region of the visual field, although as yet, no detailed neuronal implementation of this algorithm has been provided. This has not, however, limited the search for psychophysical correlates, even

though frequency-tuned adaptation phenomena do not of themselves prove that the visual system analyses stimuli exclusively on the basis of spatial periodicity.

Moreover, there is experimental data inconsistent with this prediction. Specifically, if the system possesses a number of the independent channels, each of which responds to a different band of spatial frequencies associated with a retinal image, then it would be predicted that adaptation to high contrast sinusoidal gratings should produce adaptation not only in the channel responding to its fundamental frequency, but also in those responding to its second and subsequent harmonic frequencies.

However Maudarbocus & Ruddock (1973), in an extensive and detailed invesigation, failed to observe any such secondary adaptation. Other studies have also shown that adaptation phenomena which would be predicted to occur if the system were using frequency coding, are not observed, (Henning, Hertz & Broadbent,1975; Burton, Nagshineh & Ruddock,1977).

The experiments to be reported in this chapter will examine adaptation effects produced by types of stimuli which have been shown, psychophysically to induced threshold elevation phenomena not readily explicable in terms of the Fourier model of visual processing.

This study was inspired by the psychophysical data of Naghshineh and Ruddock (1979). Nakayama and Roberts (1972) had previously shown that under some conditions contrast elevation effects are dependent not only the spatial frequency of the test and adaptation stimuli but also the relative length of the adapting bars. Burton and Ruddock (1978) later reported that this effect was length selective for gratings constructed from bar elements with a length to width ratio of less than about three to one and non-length selective for larger values.

Naghshineh and Ruddock (1978) have extended the above findings by examining threshold elevation produced by the interaction of gratings and dots. They observed the following phenomena.

Firstly, threshold elevation of test gratings can be produced by adaptation to dot patterns; this effect being selective for the width of the adapting dots when arranged in either regular rows or dispersed at random within the visual field.

Secondly, this threshold elevation produced by dots on gratings is independent of the orientation of the rows of dots with respect to the orientation of the test grating, as would indeed be predicted from the

observation that random dot patterns produce an equivalent threshold elevation for gratings, as also do regular rows of dots.

Thirdly, they report that for the converse case, adaptation to gratings did not siginificantly raise the contrast threshold for dots.

Fourthly, the threshold elevation for linear gratings produced by patterns of circular stimuli does not show interocular transfer.

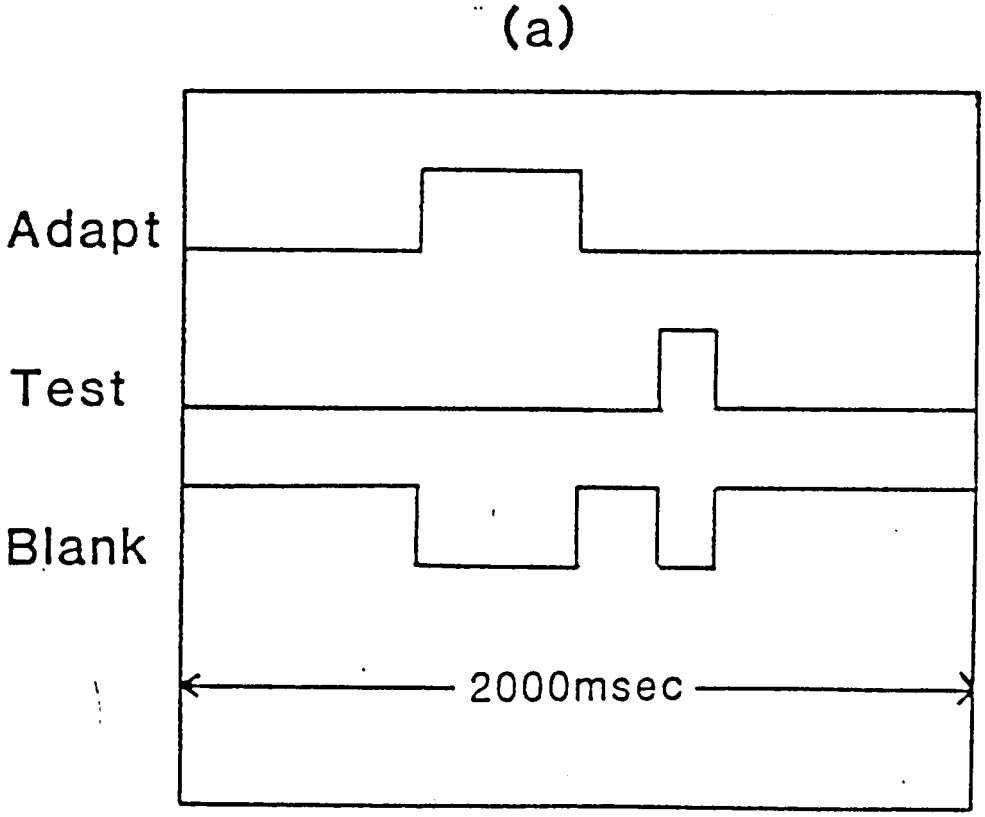
On the basis of these findings a model was proposed which, in essence, treated these threshold elevation phenomena as reflecting the properties of various types of cells within the geniculo-striate pathways, the existence of which had in turn been suggested by single unit recordings in monkey (Dow & Gouras,1974; Schiller, Finlay & Volman,1976).

Further consideration of the relative merits and possible defects of the model will be left to the discussion section of this chapter. However, irrespective of the plausibility of their model the existence of psychophysical data showing selective interactions between classes of visual stimuli warrants an electrophysiological investigation into these phenomena to determine the possible sites of these effects. Such correlates may shed light on the types of coding undertaken at specific stages within the retino-cortical pathways.

In experiment 10.1 the effects of adaptation to briefly presented pattern of dots or a square wave grating of spatial period f_a, on the CI component elicited by a test grating of period f_t was examined. In experiment 10.2 these effects are examined for dot test stimuli of variable diameter. In experiment 10.3 the orientation tuning for dot and grating adaptation was examined, whilst in experiment 10.4 the extent to which any size tuned adaptation associated with these stimuli show inter-ocular transfer was studied.

10.1. Experiment 10.1:- Dot-grating and Grating-grating adaptation

In this experiment, an adaptation procedure was used to measure the effect of pre-exposure of a dot pattern and a grating pattern on the VEP evoked by a test grating of frequency f_t over an approximately 1 octave range either side of the adaptation frequency.



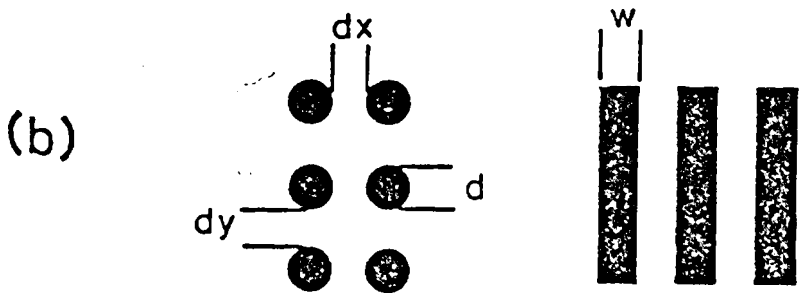


Figure 10.1a-b
Temporal relationship between adaptation and test stimuli. Stimulus configeration. See text for details.

Procedure

The frequency of the adapting grating pattern was set at 5 cpd and the diameter of the dots within the adapting dot pattern was equal to a half cycle of the grating pattern. The inter-dot spacing was equivalent to the dot diameter (see figure 10.1(b)). Thus 'd'='dx'='dy'='w'.

All stimuli were prepared from high contrast photographic transparencies and were presented in tachistoscope A. For each of the test stimuli three conditions were undertaken in random order:-

a:- test stimuli alone

b:- grating adaptation-grating test

c:- dot adaptation-grating test.

The extent of response attenuation under the adaptation conditions was then expressed as a percentage of the unadapted test stimulus response amplitude. The amplitude of each VEP peak was determined by taking the mean baseline reponse level for the period from 60 msec prior to and 30 msec after test stimulus onset (calculated by digitising the points on the CAT averager) and subtracting this value from that of the peak response to the test stimulius.

In the adaptation condition the sequence of events in each stimulus cycle is schematically described in figure 10.1(a). The duration of the adaptation pattern was set at 400 msec and that of the test pattern 150 msec. The interstimulus interval between adaptation pattern offset and test pattern onset was 200 msec, and under these conditions, subjects reported only very slight negative afterimages. In 'test alone' conditions the adaptation pattern was removed and replaced by a neutral density filter of the same overall mean luminance. The illuminance of the fields was set a 360 cdm^{-2}. Averaging commenced 100 msec prior to test stimulus onset and continued for 500 msec. The adaptation pattern extended over the whole of the 9 degree circular field at the centre of which was a small fixation cross.

Two runs of 30 sweeps were underaken.

Results

The VEP waveforms elicited by four of the test stimuli under each stimulus condition have been shown for one subject in figure 10.2. A 200 msec sample of the waveform is displayed, the start of which commences 100 msec prior to stimulus onset. These waveforms give some indication of the nature of the response, its relative size and

consistency. In figure 10.3(a) are shown the mean amplitude of CI over the range of spatial frequencies used under either grating or dot adaptation conditions. Error bars indicate +-1 SEM. It is evident that there is clear size-tuned response attenuation under both conditions; that to grating adaptation being slightly more extensive and more broadly tuned than that produced by dot adaptation. The extent of response attenuation observed here under grating adaptation is similar to that reported by Smith & Jeffreys (1978), although in the present case a more extensive range of test frequencies has been used with an adaptation frequency 1 octave above that used by the these authors. It appears that dot patterns causes size-tuned adaptation of gratings, and that this effect must reflect interactions occurring at or prior to the striate cortex.

10.2. Experiment 10.2:- Dot-dot and Grating-dot adaptation

In the following experiment the whole adaptation series was repeated, with a range of dot patterns as test stimuli; the diameter of the dots was approximately equivalent to the range of half cycles used in experiment 10.1. The same two subjects were again used.

Results

In figure 10.3(b) are shown the mean amplitude of CI recorded under these conditions. It is evident that, firstly, size-tuned attenuation for dot test stimuli is limited to the dot adaptation condition. There is no evidence of tuned attenuation with grating adaptation, rather, a general decrease in response amplitude which is independent of dot diameter is observed.

The extent of attenuation obtained with dot adaptation is slightly less for dot test stimuli, than that previously obtained with grating test stimuli. However no statistical tests were made and it is not known whether this difference is significant. The small sample size would mitigate against drawing any conclusion regarding the observed difference. The main finding is however that grating adaptation does not lead to size tuned attenuation of the VEP elicited by dot stimuli, whereas in experiment 10.1 the converse was shown to be the case.

10.3. Experiment 10.3:- Orientation specificity of dot-grating adaptation

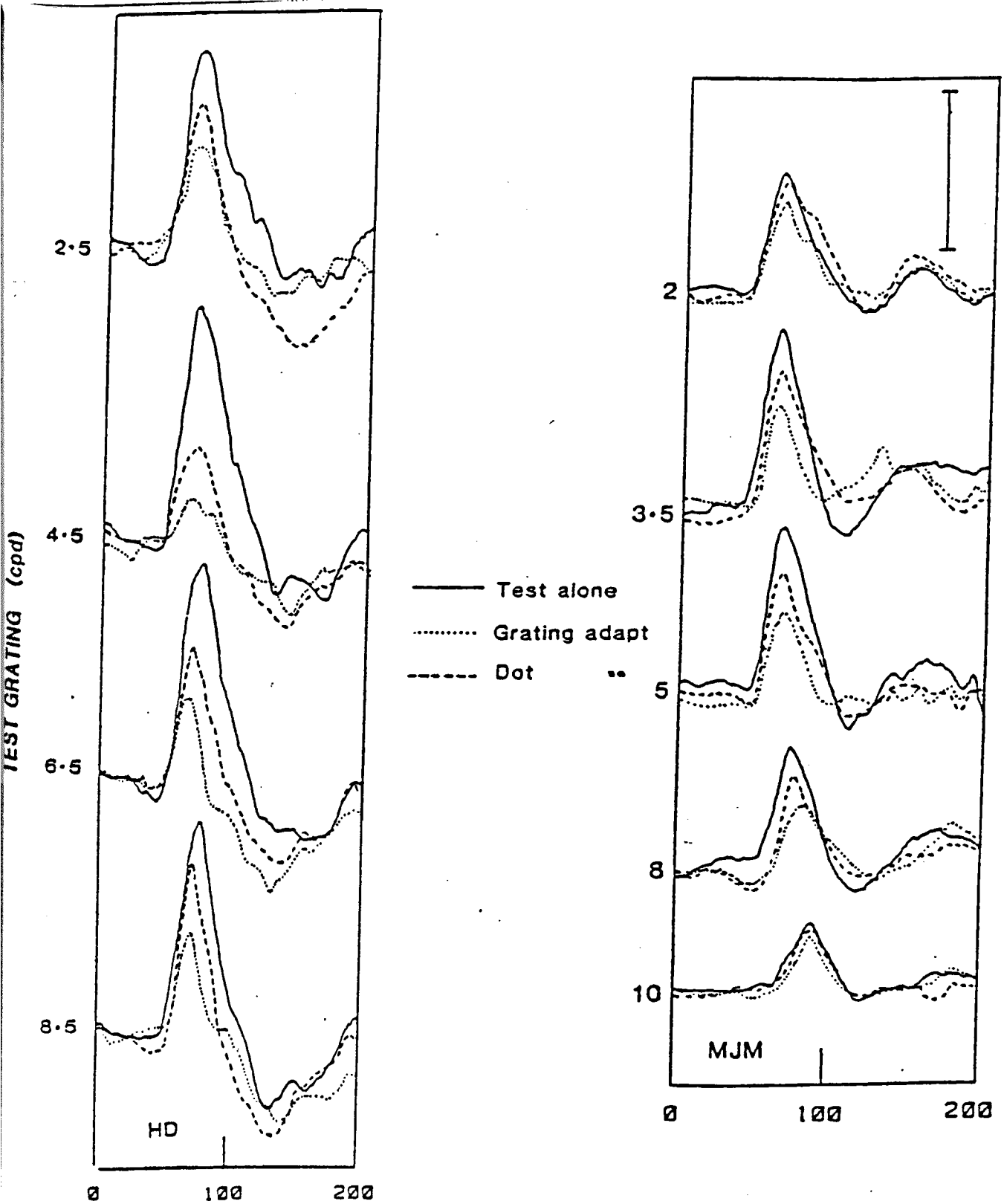


Figure 10.2

VEPs for two subjects elicited by test stimuli of differing spatial frequency under either dot or grating adaptation. The full trace is the response elicited by the unadapted test stimulus. Waveforms shown for a 200 msec period.

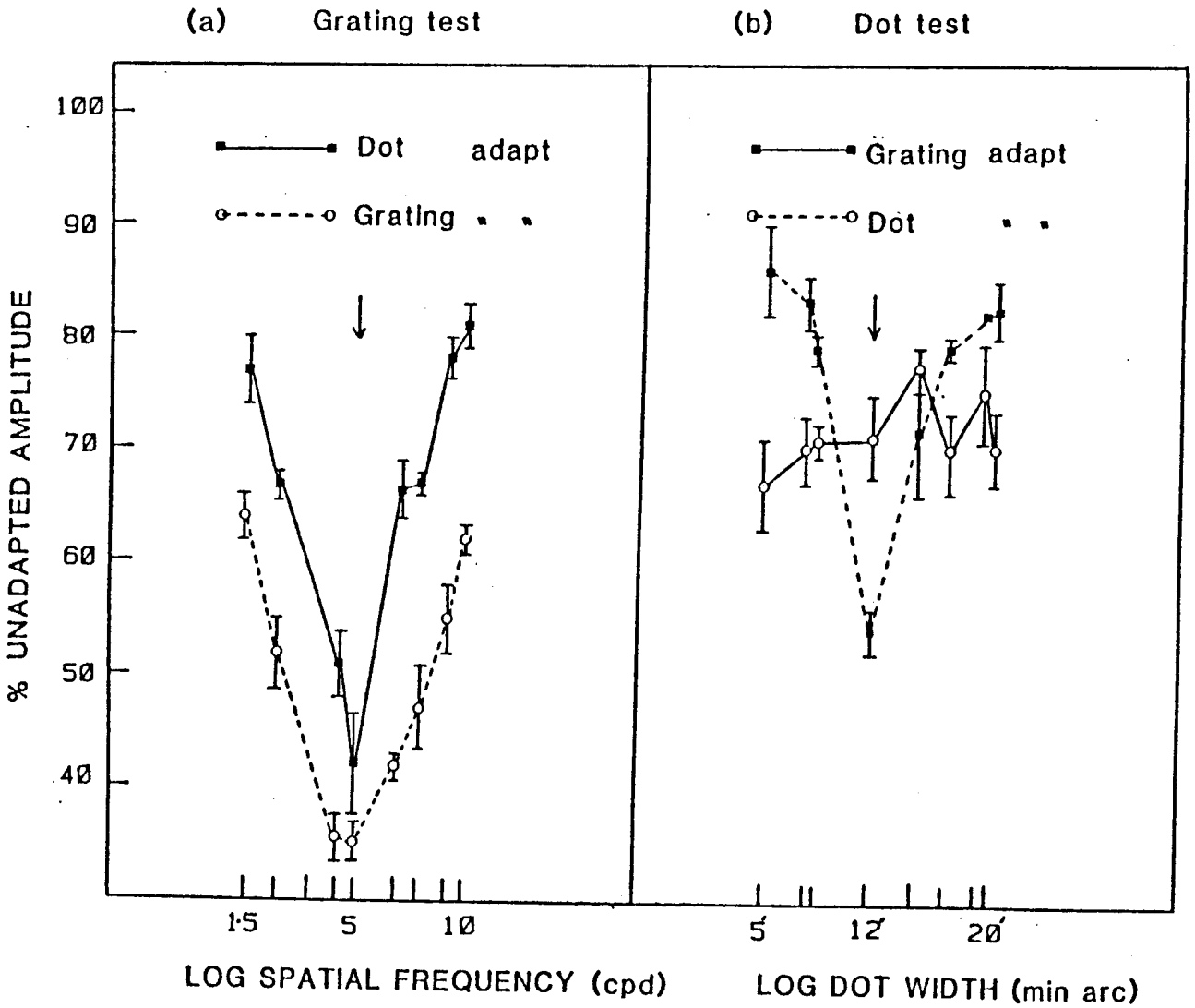
Figure 10.3a

(a):- Percentage unadapted amplitude of CI obtained under either dot or grating adaption, with a grating test stimulus. Amplitude has been plotted as a function of the spatial frequency of the test stimulus. The arrow indicates the spatial frequency of the adapting grating. The dots of the adaptating dot pattern were equal to one half cycle of the grating adaptation pattern.

(b):- Similar to (a) but in this case with a dot test stimuli with variable dot diameter.

The arrow indicates the size of the dots of the adaptation pattern. A half cycle of the grating adaptation stimulus was equivalent to the diameter of the dots of the dot adaptation pattern.

Percentage adaptation has been plotted as a fuction of log dot width of the test pattern in min of arc.


(a) Grating test
(b) Dot test
100
90
80
70
60
50
40
% UNADAPTED AMPLITUDE
Dot adapt
Grating
Grating adapt
Dot
1·5
5
10
5'
12'
20'
LOG SPATIAL FREQUENCY (cpd)
LOG DOT WIDTH (min arc)

The question that must now be asked is whether the attenuation produced by dot adaptation is dependent on the size of the dots or on their regular arrangement or orientation with respect to the orientation of the test grating stimulus. In the above experiments, patterns were composed of columns and rows of dots and thus these dot patterns may have been producing the observed response attenuation simply by acting as 'weak' gratings. If, however, these dot patterns produce their effects on the system independent of the overall orientation of the rows and colums then VEP attenuation should be observed, irrespective of the orientation of the grating test pattern.

Smith & Jeffreys (1978) have previously reported that CI shows orientation-specific adaptation for gratings of a similar orientation range to that obtained pyschophysically (Blakemore & Campbell,1969; Burton & Ruddock,1977). Thus in the following experiment I have attempted to measure the orientation tuning of dot and grating adaptation.

Procedure

Two subjects were again used. The test stimulus was a 5 cpd square wave grating presented to the left half-field. With half-field stimulation it is not possible to vary the orientation of the test stimulus without changing the effective number of grating bars within the field, and thereby increase the potency of the stimulus in evoking VEPs. Thus the orientation of the adaptation stimulus which covered the whole field were varied randomly in 10 degree steps from 0 degrees (vertical) to 70 degrees off vertical.

Results

In figure 10.4 are shown, for one subject only, the typical form of the response elicited under the specified experimental conditions.

In figure 10.5 the mean amplitude of CI has been plotted as a function of a range of orientations from 0 degree (vertical) to 70 degrees. For grating adaptation there is clear evidence of orientation-tuned attenuation, the slope of the curve levelling off at some 50 degree from the orientation of the test grating. That response amplitude does not reach the 100 % level, as might be expected if adaptation was not occurring, can be explained by the fact that brief pre-exposure to any stimulus configuration causes some decrease in

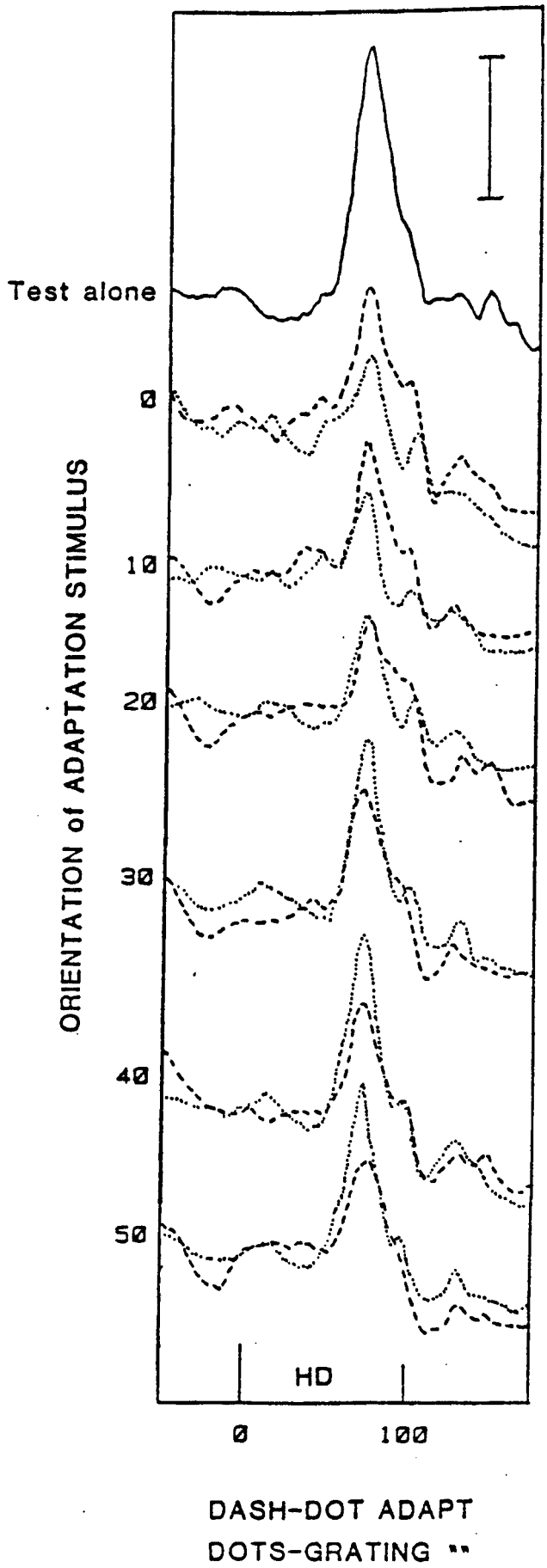


Figure 10.4

Typical waveforms obtained for one subject to dot and grating adaptation as a function of adaptation pattern orientation. The full trace is the VEP elicited by the test pattern under non-adaptation conditions.

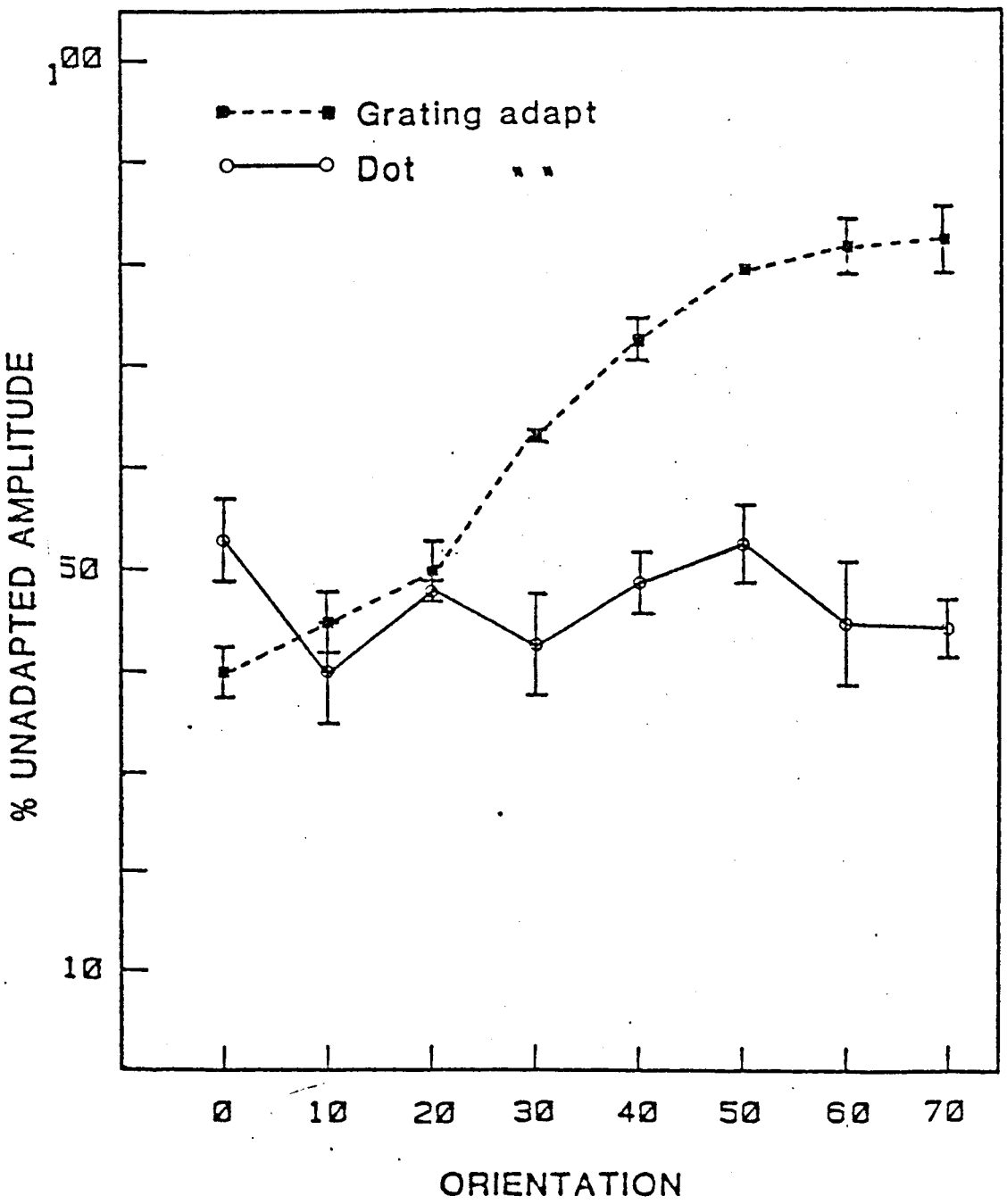


Figure 10.5

Percentage unadapted amplitude of CI plotted as a function of adaptation pattern orientation (see text). Bars indicate +- 1 SEM.

subsequent VEP amplitude. The extent of the orientation-specific adaptation observed here is similar to that reported by Smith & Jeffreys (1978) for the CI component, and by Campbell & Blakemore (1969) for steady-state potentials.

Dot adaptation however is clearly non-orientation specific remaining at a steady level of 40-50 % of the unadapted amplitude across the whole orientation range. It thus appears that these dot patterns are producing size-tuned VEP attenuation independent of their overall arrangement within the visual field. Although each dot may not be acting in isolation on the system, it is sufficiently independent of the overall configuration for the relative orientation of the array to be non critical. Dot patterns are not therefore acting on the system in the same manner as grating patterns.

10.4. Experiment 10.4:- Interocular transfer of dot and grating adaptation effects

Thus, far the results of these VEP experiments have been reasonably consistent with the psychophysical data of Naghshineh & Ruddock (1978). There is however one remaining dimension as yet unexamined and this is the extent to which these adaptation phenomena show interocular transfer. Smith & Jeffreys (1978) have previously reported that for checkerboard stimuli, interocular transfer of adaptation effects are readily observed for both CI and CII; the extent of transfer being greater for CII than for CI, which they argued (Smith & Jeffreys,1980) reflects differences in the binocularity of cells within the regions of cortex generating these components.

It seems likely that grating adaptation would similarly show interocular transfer at least for CI (CII being relatively unresponsive to such stimuli). There is much psychophysical evidence to show that contrast elevation effects do indeed readily transfer from one eye to the other, at least for subjects with normal vision (Mitchell et al,1973; Mitchell & Ware,1974).

However the interocular transfer of such phenomena does not of itself prove the existence or otherwise of certain classes of cells. The complex patterns of dendritic arborization make it unlikely that any one cell type could mediate any one particular adaptation phenomenon (see Creutzfeldt,1981). With this caveat in mind, the

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following experiment was undertaken to examine the degree of interocular transfer of dot-grating, grating-grating and dot-dot adaptation.

Procedure

Tachistoscope B was used in these experiments and two subjects again participated. The general procedure was similar to that used in each of the above experiments. In this case however the adapting stimulus was presented to the left eye and covered the whole of the 9 degree field. The test stimulus was then presented to the appropriate half field of the right eye. Because CI tends to be smaller to monocular than to binocular stimulation, the number of stimulus presentation was increased from 60 to 90 in order to give clearer responses.

Results

Figure 10.6(a) a shows the amplitude of CI plotted as a function of the spatial frequency of the test grating. It is clear that grating adaptation shows significant transfer, the effect being only 25-30% less than that obtained with binocular viewing, see figure 10.3. Dot-grating adaptation however shows significantly less transfer and, although appearing tuned, the curve is at its maximal point only 10% less than the unadapted amplitude which, given the nature of the VEP, is not perhaps significant enough to indicate the existence of interocular transfer. In figure 10.6(b) are show the mean amplitude obtained in the dot-dot adaptation condition. The curve indicates a lack of interocular transfer although there is a slight decrease in amplitude across the whole range, equivalent at the maximal point, to that obtained with dot-grating adaptation. Thus it appears that grating-grating adaptation shows ready interocular transfer, dot-grating slight transfer and dot-dot no apparent transfer at all.

10.5. Discussion

The results of these VEP experiments, albeit for a limited sample of subjects, have shown that following adaptation to both dot and grating patterns, the amplitude of CI to a test grating, of frequency f_t, is attenuated. Maximal attenuation occurs when $f_t=f_a$. Grating-grating adaptation transfers interocularly, again with maximal

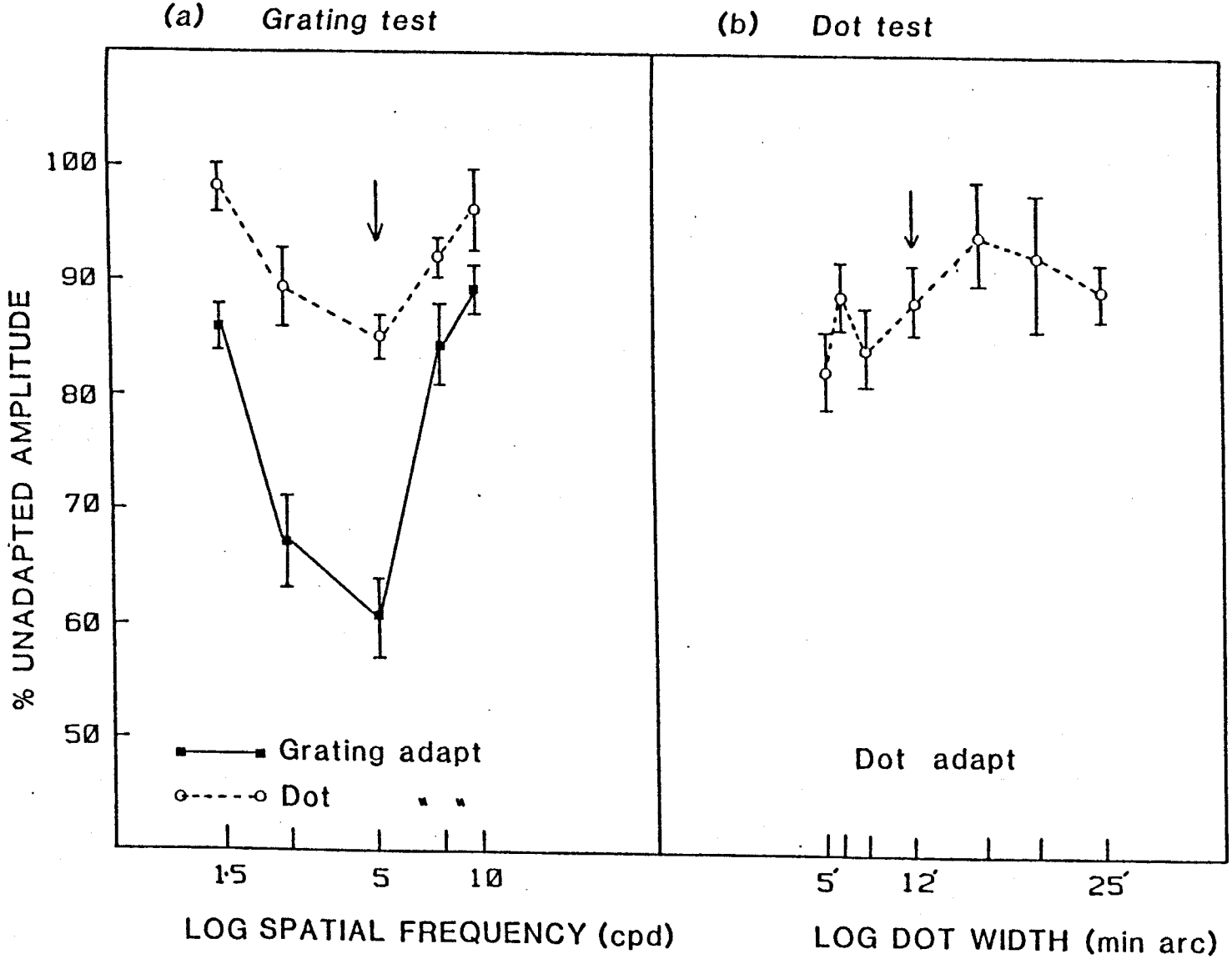


Figure 10.6

Percentage unadapted amplitude of CI under dichoptic presentation.

A = Grating test:- dot or grating adaptation see figure for key.

B = Dot test:- dot adapt.

attenuation when f_t-f_a. A weak effect under dichoptic presentation is observed with dot-grating adaptation. Dot-dot adaptation was also observed with maximal attenuation for d_t=d_a this effect does not appear to transfer interocularly as the extent of attenuation was similar for both $d_t > d_a$ and $d_t < d_a$. Grating-dot adaptation effects were not observed.

The lack of tuned interocular transfer under dot-dot adaptation was indeed unexpected, given the strength of grating-grating transfer. It is possible that the CI components of the two subjects who participated in this study have some unique properties; but this seems unlikely given the consistency of the other results (ie grating-grating attenuation) with those reported by Smith & Jeffreys (1978) for CI. If these results are repeatable in other subjects (and unfortunately this has to be left to others to do) then they suggest that the degree of binocularity shown by these VEP components (which is assumed to reflect the degree of binocularity in the underlying cortical generators) are stimulus specific. Thus Smith & Jeffreys (1979) conclusion that 50% of human striate cells are monocularly driven may need revision.

These VEP data are, to a first approximation, consistent with the psychophysical findings of Naghshineh & Ruddock (1978) in regard to the properties of the so called 'length' and 'non-length' selective mechanisms. These authors propose a model of the visual system (retino-striate pathways) in which the initial channels representing the retino-geniculate pathway are purely monocular, transmitting signals evoked by both dots and bar stimuli. At the lateral geniculate body, a major reorganisation is predicted to occur resulting in two semi-independent channels which project to the striate cortex. The first of these channels is exclusively monocular and sensitive only to dot stimuli and forming part of the length selective mechanism. This channel does not receive input from other channels of either ipsilateral or contralateral origin.

The second channel, which is non-length selective receives input from both the ipsilateral retino geniculate channel and the contralateral non-length selective channel. Orientation-selectivity within this channel is determined by activity prior to the level at which adaptation occurs. This channel thus receives binocular input from bar stimuli and monocular input from spot stimuli. Thus far, the model merely descibes the pyschophysical data and

raises little debate. However the predictions as to the neuronal substrate of these hypothesised channels are more controversial. Naghshineh & Ruddock do themselves suggest that the properties of the length selective channel suggest the involvement of a population of non-orientated cells such as reported by Dow & Gouras (1973) and Schiller et al (1976). These cells predominate in layer IVb&c of the striate cortex of monkey and have been thought to be part of the initial stage of cortical processing because they receive direct input from geniculate afferents (Hubel & Wiesel,1965). Indeed there has been debate as to whether the recorded responses were indeed cellular in origin or merely the response of afferent fibers since they bore a remarkable resemblance to that observed for geniculate cells. The neuronal correlates of the non-length selective mechanisms is thought by the above authors to be a class of simple type cells having orientation preferences and spatial frequency selectivity similar to that observed psychophysically (Maffei,1973).

At this point the model becomes controversial, because length selectivity (end-stopping to use single unit terminology) is generally considered a property of complex amd hypercomplex cell types (Hubel & Wiesel,1972; but see chapter 1). The various components of the model seem therefore at variance with the underlying functional physiology, which suggested that features such as length selectivity occur later in the chain of cortical processing, indeed that they receive input from those non-length selective mechanisms such as simple cells (Hubel & Wiesel,1972; though see Stone et al,1979). However, as length selective adaptation does not show interocular transfer it seem unlikely that it can be associated with the complex/hypercomplex population (Hubel & Wiesel,1972).

Although the present VEP data cannot directly answer the problems posed by the stimulus-specific adaptation phenomena, they do suggest that interactions, both dependent and independent of stimulus length and orientation, occur at or prior to the striate cortex. However in the light of our limited understanding of orientation coding (Blakemore,1981; Dow et al,1981; Tsumoto et al, 1978) and of the determinants of ocular dominance (Sillito,1980; Hammond & Mackay,1977) within the striate cortex, it seems somewhat optimistic to postulate that specific types of psychophysical phenomena of the type discussed are determined by a particular class of cortical cell. Whatever their exact nature it can be stated that the neural

interactions underlying the effects reported in these experiments occur at or prior to the level of the striate cortex and that they show specific stimulus type interactions that are size dependent in a manner that would not be predicted from the notion that the visual system analyses retinal images in terms of their Fourier components (Naghshineh & Ruddock,1978).

Recent single unit data from the striate cortex of the macaque (DeValois,1978) has been interpreted as showing that simple cells code the Fourier components of stimuli falling on their receptive field; a conclusion similar to that drawn by Pollen and associates (but see MacKay,1981). However, the advocated Fourier model requires some form of non-local integration across the whole of the visual field since, by definition, it is a global process. The receptive fields of simple and complex cells are not global in any sense. The alternative notion of a 'piece wise' Fourier transform simply avoids the issue as it does not specify how these multiple pieces of Fourier analysis are formed into a global map. If it is suggested that the process of synthesis takes place at a higher cortical level, such as extrastriate or inferotemporal cortex, where receptive fields are known to be large (Zeki,1978; Gross 1972; Gouras & Kruger,1978; Fisher et al,1981), the suggestion would clearly conflict with the single unit data from these regions, which show conclusively that gratings and similar stimuli with a simple contrast profile are ineffective in driving these cells.

The notion that cortical cells or populations of cells form frequency selective channels, each performing a Fourier analysis of a limited region of visual space is both theoretically impracticable and not proven by the experimental data. Fourier analysis as a mathematical technique assumes a completely linear system and the visual system is clearly non-linear, even at retinal level (Burton,1974). That psychophysical and electrophysiological data appear consistent with the predictions of the theory, particularly near threshold, is a fortunate coincidence as it allows the use of the sophisticated methods of analysis based on the theory. Cortical cells may be bar detectors under one condition and edge detectors under another, and it is likely that the behaviour they display is determined by patterns of intercortical wiring, as suggested by the work of Hammond & Mackay (1977) and Movshon (1975).

Further experiments, both psychophysical and electrophysiological, will be needed to determine in greater detail the neuronal correlates

of the types of stimulus dependent adaptation phenomena reported in this chapter. Such experiments might profit from the use of coloured stimuli of various wavelength combinations as the single unit data of Gouras & Kruger (1979) from the macaque suggest that the receptive field organisation of cortical cells are modifiable, according to the distribution of wavelength differences across them. It would thus be interesting to know whether the types of length and non-length dependent adaptation phenomena observed with luminance contrast stimuli also occur under isoluminant colour contrast, since Gregory (1980) reports that under these conditions classic visual illusions are not observed.

Chapter 11:- Colour contrast VEPs.

Introduction

Colour vision in man and other primates is generally said to be trichromatic, since only three suitably chosen wavelengths are required to produce all colour sensations (Maxwell,1885). Such trichromacy is fundamentally dependent upon the photopigment molecules within the outer segments of the cone receptors, which are densely packed within the foveal region of the retina.

There appear to be three cone types popularly called the Red, Green and Blue cones (DeValois,1966; Gouras,1970). However this classification is misleading for the following reason. The three cone types possess photopigments with peak absorbtion in the region of 445, 540 & 570nm respectively, with the latter two capable of absorbing across the whole of the visible spectrum, rather than over a limited range. The cone which absorbs maximally at 570nm has been called the "red cone" because its peak sensitivity occurs at a longer wavelength than that of the peak sensitivity of the two other cones; but in fact it is more sensitive to that region of the spectrum normally seen as green (530nm) than that seen as red (610-700nm). Rather than defining the cone types by the hue adjectives which imply that they are colour receptors, the terms 'L', 'M' & 'S' cones will be used to denote three cone types with maximum sensitivity at 570, 540 & 445nm respectively.

One method of estimating the peak absorption of cones has been to study the spectral sensitivities of colour defectives. Wilmer (1965) for example measured the spectral sensitivity of dichromats of the protonopic, or the deutronopic variety. Utilising the phenomena of 'small field tritonopia' (see Ruddock & Burton,1972; Macleod,1980), Wilmer found that the dichromat showed the properties of a monochromat, with the protonopes having a peak sensitivity at 540nm, and the deutronopes a peak at 570nm, consistent with the peak sensitivities of the 'L' and 'M' cones respectively.

Blackwell & Blackwell (1961) in a study of monochromats, who appeared to have only 'S' cones and rods, obtained a peak sensitivity measure of 440nm, consistent with that predicted for the 'S' cone.

Estimates of receptor absorption characteristics have also been made by electrophysiological methods. DeValois (1965) reports that by using the adaptation technique of Stiles (1949), it was possible to reveal cone input to various types of opponent cells. Maxima were found at 440, 540 and 570nm respectively. The same technique has been used by Michael (1965) to reveal cone types with maxima of 460 & 525nm in the ground squirrel. These psychophysical and electrophysiological techniques are however limited, in that cone spectral sensitivity is measured indirectly. A more direct method has been the microspectrophotometry of individual receptors extracted from the enucleated eye. MacNichol (1965) has applied this technique to the macaque and reported peak sensitivities of 445, 535 & 570nm for the three cone types. Bomaker & Dartnell (1980) in a detailed study of a single human retina report peak sensitivities of 420, 533.8 & 562.8nm.

Clearly it would be inaccurate to ascribe the adjectives red, green and blue to the cone types. The perception of hue and of hue differences must be the result of neural interactions within, and between, the channels fed by the 'L' ,'M' and 'S' cones. Single unit evidence of such interactions is now overwhelming, at least in the primary visual pathways of monkey, (De Valois 1965, 1973; Gouras,1970, 1973; Creutzfeldt et al,1979).

The experiments reported in this chapter will examine the properties of the CI and CII components elicited by patterns of pure colour contrast. It is hoped that by comparing the VEPs elicited by such stimuli with those evoked by patterns of luminance contrast, some clues will be obtained as to the types of processing undertaken by those regions of human visual cortex generating these components. It will then be possible to compare the properties of these VEP components with those of single units, recorded in monkey visual cortex with a view to relating these two types of electrophysiological activity. A comparison between the temporal properties of colour contrast and luminance contrast VEP will also be undertaken.

The clearest evidence of the importance of wavelength distribution across the receptive field of single units has come from the study of the LGN, and in particular from its parvocellular layers (PCL) in the monkey. Hubel & Wiesel (1972) report the existence of PCL cells, which show true wavelength opponent behaviour. Accordingly, these cells were termed 'spectrally opponent' as they could be shown for example to be maximally excited by wavelengths of 500nm and maximally inhibited by

wavelengths of 630nm. A unit having this type of response property can be considered (DeValois,1966,1967) a green-excitatory, red-inhibitory (+G-R) cell. In the macaque DeValois (1965) has revealed four types of spectrally opponent cells having spatially organised receptive fields with wavelength-dependent excitatory centres and inhibitory surrounds. These were thought to form two separate colour systems in the primate. The Red-Green system composed of those cells termed (+R-G) and (+G-R), which cross from excitation to inhibition at approximately 560nm, and the Yellow-Blue system which crosses from excitation to inhibition at wavelengths below 560nm. Other units were reported to be spectrally non-opponent, that is, they responded to an appropriately positioned stimulus of any wavelength, and were thus considered to have little role in the signaling of colour or of colour contrast. Spectrally non-opponent cells form a minority in the parvocellular layers; DeValois reports 70% opponent cells as compared to 30% non-opponent cells.

In the magnocellular layers (MCL) the converse is the case and the ratio of non-opponent to opponent cells is greater; the former have been termed the 'broad band' cells to characterise their indiscriminate sensitivity to varying wavelength stimuli. Indeed, Gouras (1970) has suggested that the magnocellular layers form part of a totally separate retino-cortical system, processing signals from both rods and cones and fed by larger ganglion cells.

The assumption that the parvocellular layer of the LGN forms part of a colour signalling system is supported by the work of Creutzfeldt et al (1979), although they suggest a different classification from that of De Valois, in that the response to white light is considered. A further difference between Creutzfeldt et al's classification and that of De Valois is that whereas the latter considered the receptive field properties of PCL cells to be entirely concentric, the centre being fed by one major cone type and the inhibitory surround by another to form a receptive field with an "opponent organisation", the data of Creutzfeldt et al (1979) suggest that for many opponent cells there is a concentric superimposition of excitatory centre and inhibitory surround, the extent of which is not fixed but is itself wavelength dependent. Indeed the data suggest that the suppressive surround of PCL cells may be determined by input from all cone types as its spectral sensitivity was found to be wider than any individual receptor type. The implication of this finding is that the receptive field profile of PCL cells may vary according to stimulus wavelength and size. The

balance of excitation and "suppression" shown by any particular cell is therefore more variable than would be suggested by the DeValois model of receptive field organisation. This notion is supported by the work of Kruger (1979).

The afferent fibers from colour opponent cells in the LGN project to layers IVcb and V, of the striate cortex. Given the percentage of opponent cells within LGN it was surprising that those in striate cortex respond indiscriminately to stimuli of differing wavelength (De Valois,1973). For example, Hubel & Wiesel (1968) report that from a sample of cells in striate cortex of macaque, only 25% of the simple and 10% of the complex cell category showed colour selectivity. Later studies (Boles,1971; Poggio, Mansfield & Silitoe,1971) reported a higher proportion of wavelength selective cells and recent studies, in particular those of Gouras & Kruger (1979) and by Michael (1978ab), have shown that the previously reported absence of colour sensitive cells in monkey striate cortex resulted from the fact that many have a 'concealed' colour opponency which is revealed only under specific conditions.

The data suggests, therefore that whilst single striate cells may not be wavelength selective in the sense that they respond only to optimally orientated stimuli of limited spectral content, they do have a spatially dependent colour opponent receptive field organisation.

11.1. VEP studies of colour processing

Previous VEP studies of colour processing can be divided into two main groups; those which have used unpatterned monochromatic stimuli as the evoking stimulus; and those in which patterns of chromatic contrast have been used. Those studies that fall into the former group have attempted to describe the wavelength dependent characteristics of the VEP (White,1977; Yamonka,1973); they follow the earlier studies by Shipley et al (1965) and Ciganek & Ingvar (1969) who had sought to relate peaks in the VEP waveform evoked by isoluminant colour fields to different cone mechanisms. Shipley for example classified VEP waveforms into three types which corresponded roughly to the spectral region 380-540nm, 590 and 640nm, whilst Ciganek relates wavelength differences to waveform variations at 453-475, 551 and 615nm and suggests that his data give clear evidence of trichromatic processing in the visual cortex of man.

However the evidence previously reviewed clearly shows that the photoreceptors in man have peak sensitivity at 445, 540 and 570nm. Secondly, if the human visual cortex is similar in its organisation to that of the monkey, one would not expect evidence of trichromacy to be obtained from the flashing of structureless, monochromatic stimuli. Thirdly, these studies have failed to report any evidence of either a retinal or electrode position dependency of these so called wavelength specific components. It is unlikely therefore that they reflect in any meaningful way, the processing of colour within the human visual cortex.

The second approach to the VEP study of colour processing is most clearly represented by the work of Regan (1972, 1973). McCree (1960) had shown the importance of colour contrast boundaries between bipartite fields for the perception of hue differences, (see Boynton,1979). Similarly, luminance contrast VEPs are maximal in amplitude when elicited by stimuli rich in contrast borders and it would be expected that, if contrast borders are such potent stimuli for the visual system, then patterns of pure colour contrast should produce VEPs. Regan (1972) has shown that this is indeed the case and his data suggests that the human visual cortex contains mechanisms excitable by wavelength differences irrespective of the luminance contrast. Regan & Spekreijse (1975) have further shown that, for patterns of red/green contrast, the large VEPs elicited in subjects with normal colour vision are absent from deuteronopic subjects.

However, it is not known whether the transient VEPs recorded by Regan & Spekreijse were the CI or CII components, or whether indeed the VEPs elicted by colour contrast stimuli come from the same region of cortex as those elicited by patterns of luminance contrast. The experiments of this chapter will attempt to clarify the issue.

Futher support for existence of colour coded cells within human visual cortex has come from psychophysical studies of colour-contingent aftereffects, of which the McCollough effect has been the most extensively researched. (McCollough,1965; Lovegrove & Over,1972; Breitmeyer & Cooper,1972; MacKay & MacKay,1975; Skobo,1980). For a detailed reveiw of the nature and properties of the McCollough effect, see MacKay (unpublished doctral dissertation, Keele,1978).

11.2. Experiment 11.1:- Colour specificity of CI.

Procedure

Tachistoscope C was used for these experiments (see figure 2.2 chapter 2). A stimulus cycle consisted of a blank field of variable colour (depending on conditions) switching with a patterned field, the background of which was similar in colour to the blank field into which the pattern elements of the opponent colour were presented. A variety of colour contrast relationships were used, for example, the blank field may have been yellow and the patterned field set to contain green squares on a red background. Alternatively, the blank field was red or green corresponding to the background field of the colour contrast pattern.

The field was circular and subtended 3 degree, the surround was black. For half field stimulation a field stop was inserted in front of the appropriate half field thus reducing the effective area of visual stimulation to 1.5 degree. A transparent negative containing a small cross positioned in the centre of the blank field provided a fixation point.

Equating the field luminance

Coloured beams were produced by inserting Kodak Wratten filters in front of the appropriate light boxes. Equating different wavelength stimuli in terms of their relative luminances is a notoriously difficult problem (Regan,1972; Boynton,1978). The standard psychophysical technique of heterochromatic flicker photometry was used here. The patterned mirror was removed and a plain half silvered mirror inserted. Fields 1 and 2 are then alternated at a frequency of 11-12 Hz. If the luminance ratio of the two colour fields is unbalanced a strong impression of flicker is obtained. The subject's task was to adjust, by means of neutral density filters and a rotatable polaroid, the intensity of field 1 until the impression of flicker is minimal. At the point of minimal flicker the two beams are considered to be isoluminant. Having equated the luminances of the fields the patterned mirror was re-inserted.

A range of patterned colour contrast combinations were presented at a number of presentation times (see figure captions for details). An attempt was made to determine the extent to which colour contrast VEPs are independent of luminance contrast, because if pattern specific VEPs

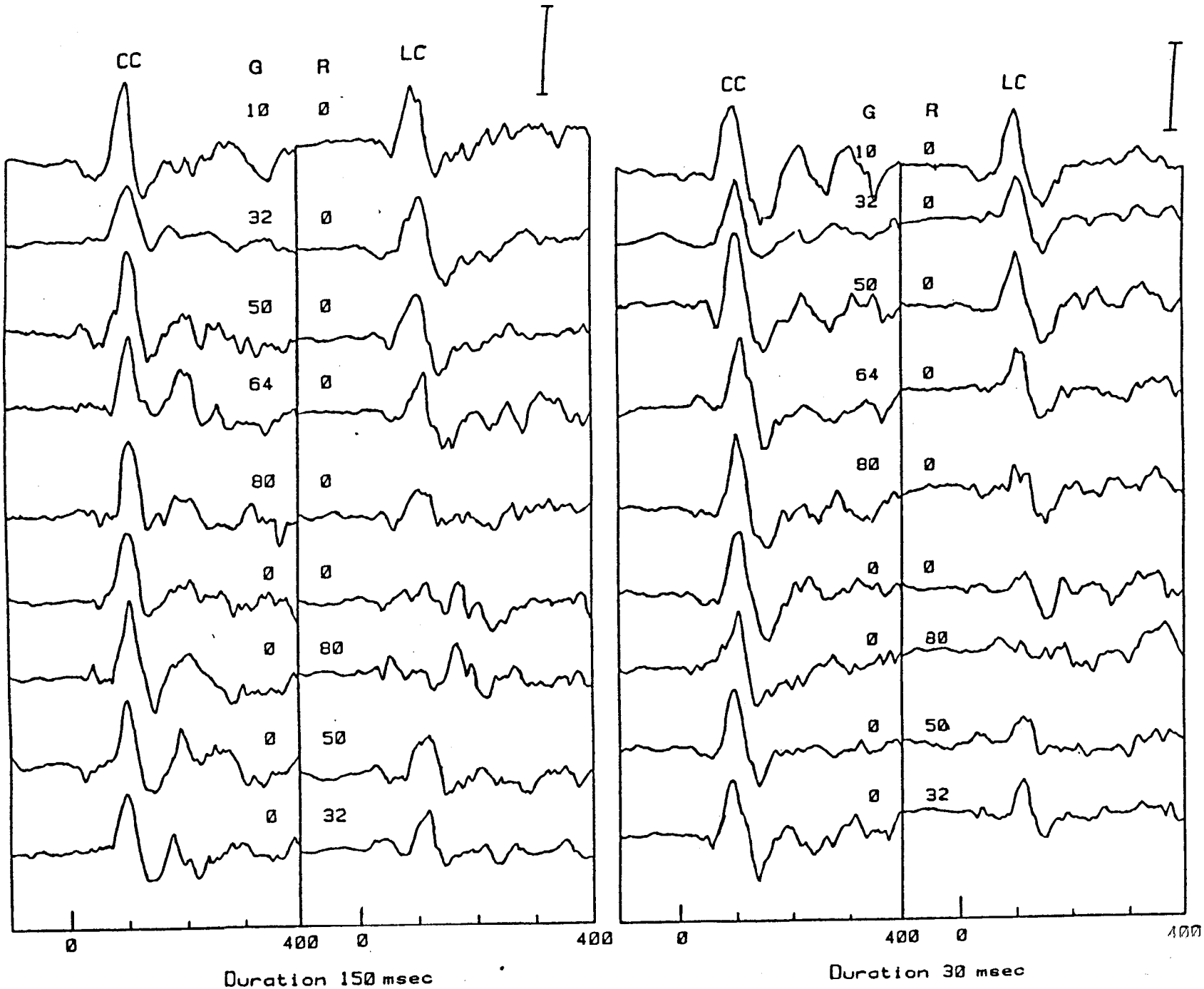
Figure 11.1

Waveforms for one subject recorded under colour or monochromatic luminance contrast stimulation for durations of :- 30 msec and 150 msec.

In column one, marked CC the pattern consisted of green squares on a red background. In column two, marked LC, the stimulus pattern was a composed of red squares on red background. The letters G & R indicate the red background field, and the green field illuminating the pattern elements (in the monochromatic luminance condition the green filter was removed and replaced by a red one. Thus in the LC condition G should be read as R.)

The values of neutral density filter, (percentage tranmission), inserted into the field illuminating the pattern elements or the background field are given in the centre of the figure. Thus at 0-0 the pattern elements (green or red) and the background will be isoluminant. For values above 0-0 the illumiance of the background field remains constant, and that of the pattern elements will be progressively reduced. For values below 0-0 the pattern elements will remain of constant luminance and the background field will be progressively reduced.

Each waveform is the sum of seven runs of 8 sweeps (see text for details).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R
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32
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50
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80
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80
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400
0
400
Duration 150 msec
CC
G
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LC
10
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32
0
50
0
64
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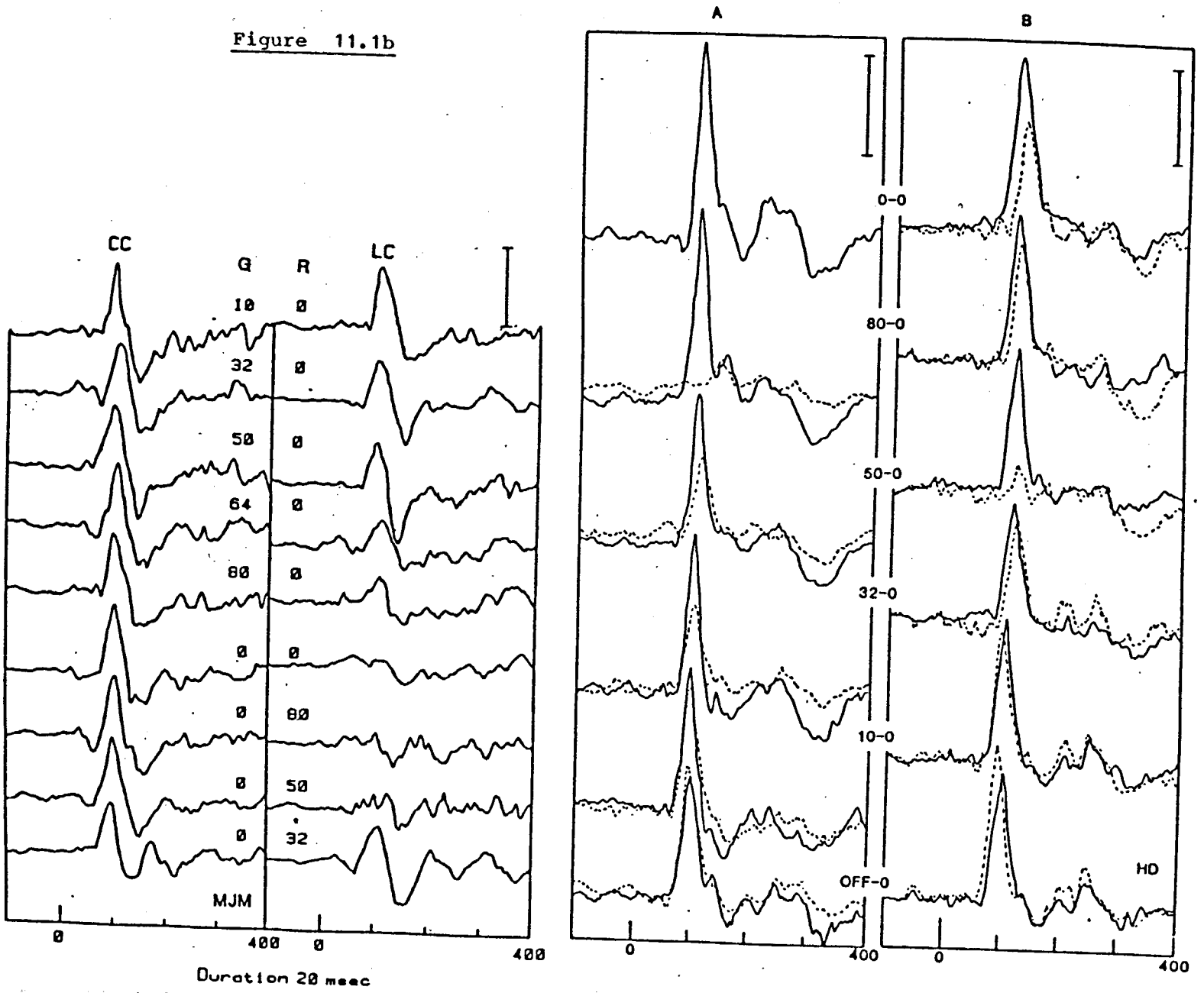
Duration 30 msec

Figure 11.1b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400
Duration 20 msec
A
B
0-0
80-0
50-0
32-0
10-0
OFF-0
HD
0
400
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400

Figure 11.2

Taken from Gouras & Kruger (1978).

Responses of single units in striate cortex of macaque, under comperable conditions to that used in the present VEP experiment. These units respond to both luminance contrast and isoluminant colour contrast, with little modulation of peak discharge amplitude in the case of the latter, similar to the effect reported here for CI.

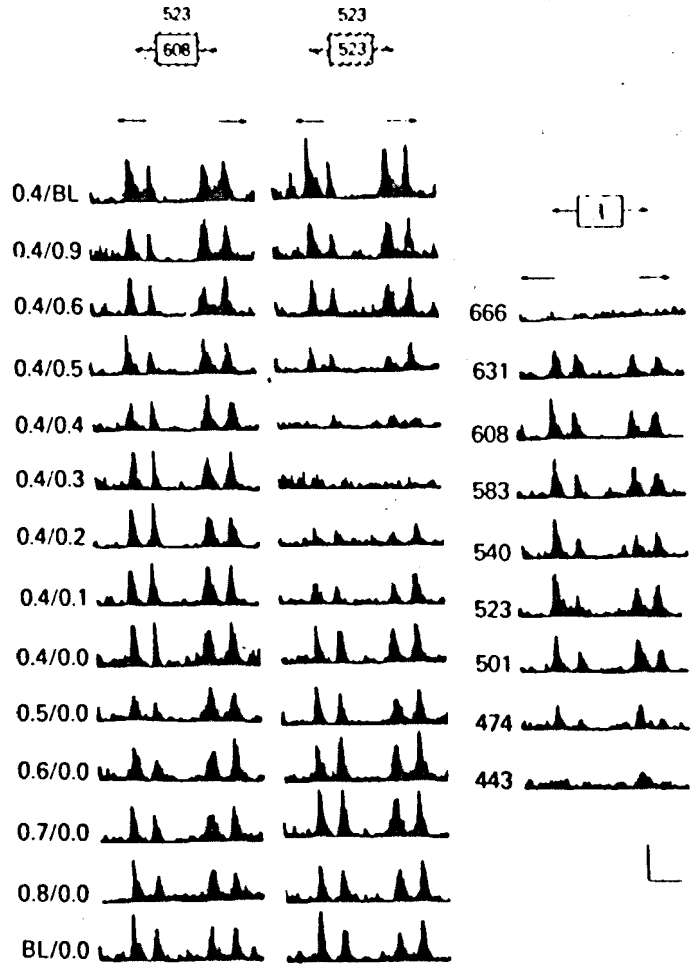


FIG. 2. Frequency-response histogram to moving stimuli of a cell that responds similarly to both forms of luminance contrast. The cell is located in layer 3 of striate cortex, has orientation selectivity, and responds well to either eye. The right eye is occluded here. The rectangle stimulus is 52′ x 1.3′ and moves horizontally along its axis. Luminance contrast is varied in the heterochromatic (left) and homochromatic (middle) situation. Numbers at the left of each response indicate the amount of neutral density in the slit (left of slash) and in the background (right of slash); therefore, the slit is maximally brighter than the background for the uppermost and maximally darker for the lowermost set of responses. The symbol, BL, signifies that one of the two beams, either stimulus or background, has been occluded (see Fig. 1). The wavelength, in nanometers, for slit and background is shown above. Steps are the same for both left and middle sets of responses. The right set shows responses of the cell to the same slit presented as different wavelengths (at left) brighter than the background. The calibration at the lower right signifies 50 impulses/s vertically and 0.8 s horizontally. For this and subsequent illustrations (Figs. 3–6), the stimulus is centered over the cell's receptive field and moves back and forth across the center at approximately 1° s^{-1} over an angle of 2°; the length of each trace is 4 s.

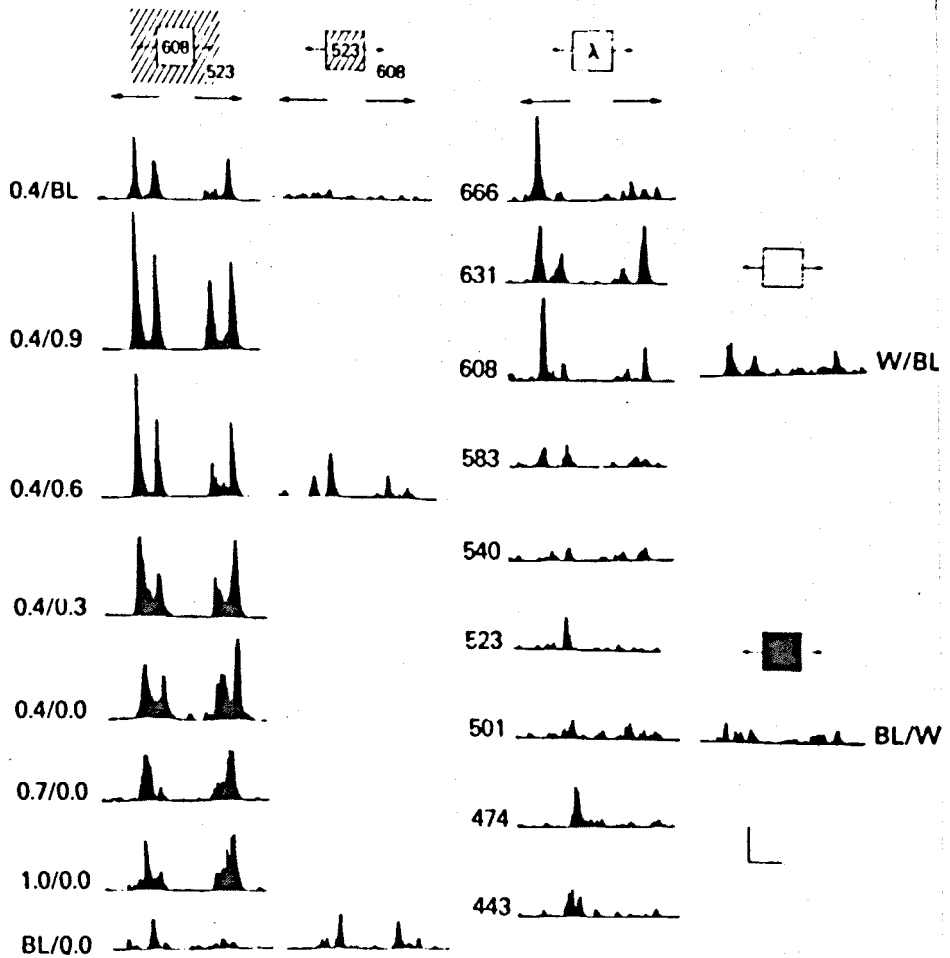


FIG. 5. Frequency-response histograms to moving stimuli of a color contrast-selective cell. It is located in layer 3 of area 18, has weak orientation selectivity and a binocular input. The left eye is occluded here. The stimulus is 28′ x 28′. This cell is excited by the left edge of a red rectangle and, to a lesser extent, by the right edges of red and green rectangles. The largest responses are obtained for a color contrast at about minimal brightness contrast. These responses are larger than the sum of responses to the monochromatic stimulus components. The calibration at lower right signifies 50 impulses s^{-1} vertically and 1 s horizontally.

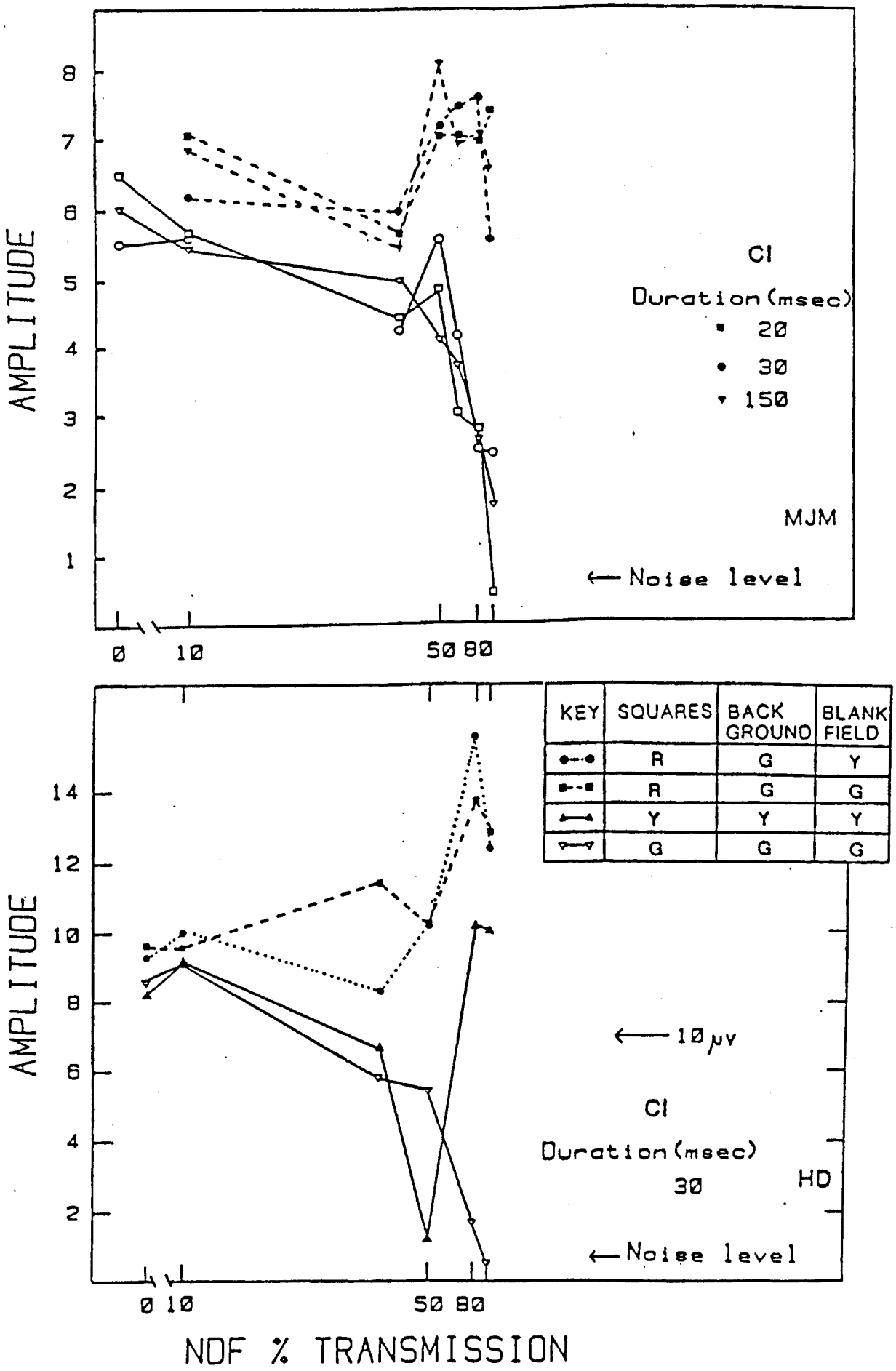


Figure 11.3

Plots of CI amplitude as a function of pattern contrast (percentage neutral density transmission) for both colour and luminance contrast stimulation.

For subject HD, bottom graph, the dashed and dotted trace are for colour contrast stimulation. The full trace marked by the (▲) illustrates the case where the heterchromatic luminance

are elicited by isoluminant contrast, those mechanisms generating them can only be responding to wavelength differences.

Two conditions were utilised; firstly, colour contrast patterns were presented and VEP recorded to the progressive increase in luminance ratio of pattern elements and background field; secondly, the wavelengths of each field were matched and the illuminance of the pattern elements progressively increased or decreased. Maximum luminance contrast was obtained by occluding the light beam illuminating the patterned field.

Two subjects were used for the study of CI and two subjects for the study of CII. In the case of the latter, upper or lower half field stimulation was used and the VEP recorded from a midline electrode 4cm above the inion with reference to the right ear.

Results

The results have been shown both as actual VEP waveforms and as plots of VEP amplitude as a function of pattern element contrast for both colour contrast and monochromatic contrast stimuli. The results for each subject will be considered separately as stimulating conditions differed slightly for each. Typical VEPs elicited by colour and luminance contrast patterns of variable contrast ratios at three durations 20, 30 and 150 msec are shown in figures 11.1.

Two main features are evident in these waveforms. In the monochromatic condition (red-red), as the luminance contrast is progressively decreased there is both a systematic decrease in peak amplitude and an increase in peak latency up to the point at 0-0 where the response cannot be differentiated from the background noise level. The VEPs elicited under these conditions are similar to typical achromatic luminance contrast VEPs in that they have a magnitude and latency dependent on pattern contrast. This conclusion can clearly not be drawn for the responses evoked by colour contrast stimuli. A progressive reduction in luminance contrast does not result in any decrease in VEP amplitude. The main effect of a reduction in luminance contrast under these conditions is to produce a small but progressive increase in peak latency of approximately 15 msec from maximal luminance contrast to isoluminance, an effect that is observed at all durations. The waveforms shown in this figure should be compared to those of single unit discharges (figure 11.2), from a colour contrast sensitive cell located in foveal striate cortex of the macaque.

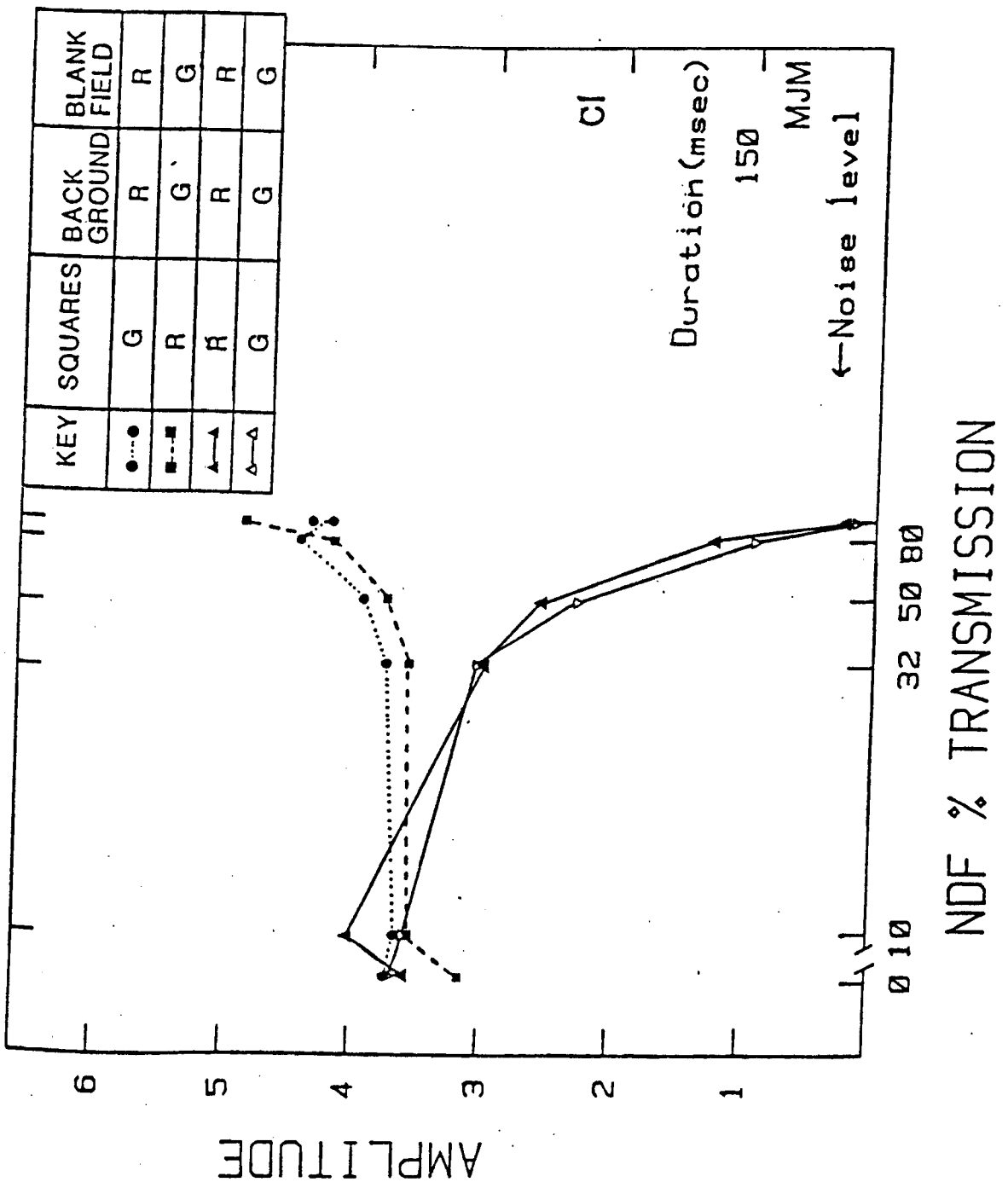


Figure 11.4

Plots of CI amplitude as a function of pattern contrast for either colour or monochromatic luminance conditions.

Shown in this figure are the amplitudes of VEPs recorded to a variety of colour contrast combinations. The Key is given in the figure. Colour contrast data are indicated by the dashed and dotted trace, monchromatic luminance contrast by the continuous trace.

In figure 11.3a peak amplitude is plotted as a function of the percentage transmission of a neutral density filter inserted into the pattern element field under either the colour contrast or the contrast monochromatic condition. At 0-0 on the abcissa, the field is isoluminant whereas at 0 the pattern is at maximum luminance contrast. Several features are evident. For the monochromatic luminance contrast condition the curve is fairly flat from maximum contrast to contrast of approximately 50%, whereafter it systematically decreases, being reduced to noise level at isoluminance. The function is similar to that which would be predicted if the stimulus parameter determing peak amplitude was luminance contrast, since under standard conditions the peak saturates at approximately 50 % contrast.

VEPs elicited by colour contrast behave in the opposite manner, showing a fairly flat function up to 50 %, with no minimum, although the overall amplitude is greater than that obtained for monochromatic luminance contrast. However, as luminance contrast is minimised to approach isoluminance, the amplitude of the VEP show a distinct increase. These results are independent of the organisation of the colour contrast pattern as is shown by figure 11.4 where VEP evoked by green squares on red background or red on a green background have been plotted along with the appropriate monochromatic control conditions. The results are consistent with those shown in figure 11.3a; again there is a slight increase in the amplitude of colour contrast VEPs at and around isoluminance, whereas monochromatic stimuli produce VEPs having similar properties to those elicited by achromatic contrast stimuli.

In figure 11.5b VEPs elicited by either colour contrast or monchromatic contrast stimuli are shown for a second subject. The sensitivity of the underlying cortical generator to isoluminant stimuli is clearly evident. In column A are shown the VEPs elicited by red squares presented on a green background along with the VEPS elicited by the appropriate monochromatic controls. Consistent with the data of the previous subject, monochromatic luminance contrast stimuli evoke VEPs similar to those of achromatic stimuli of variable contrast. There is a progressive decrease in amplitude and increase in peak latency as contrast in reduced. Again there is no such comparable effect for VEP evoked by colour contrast stimuli; the latency of the peak increases by approximately 15 msec from maximum luminance contrast to isoluminance, similar to the value observed for subject MJM.

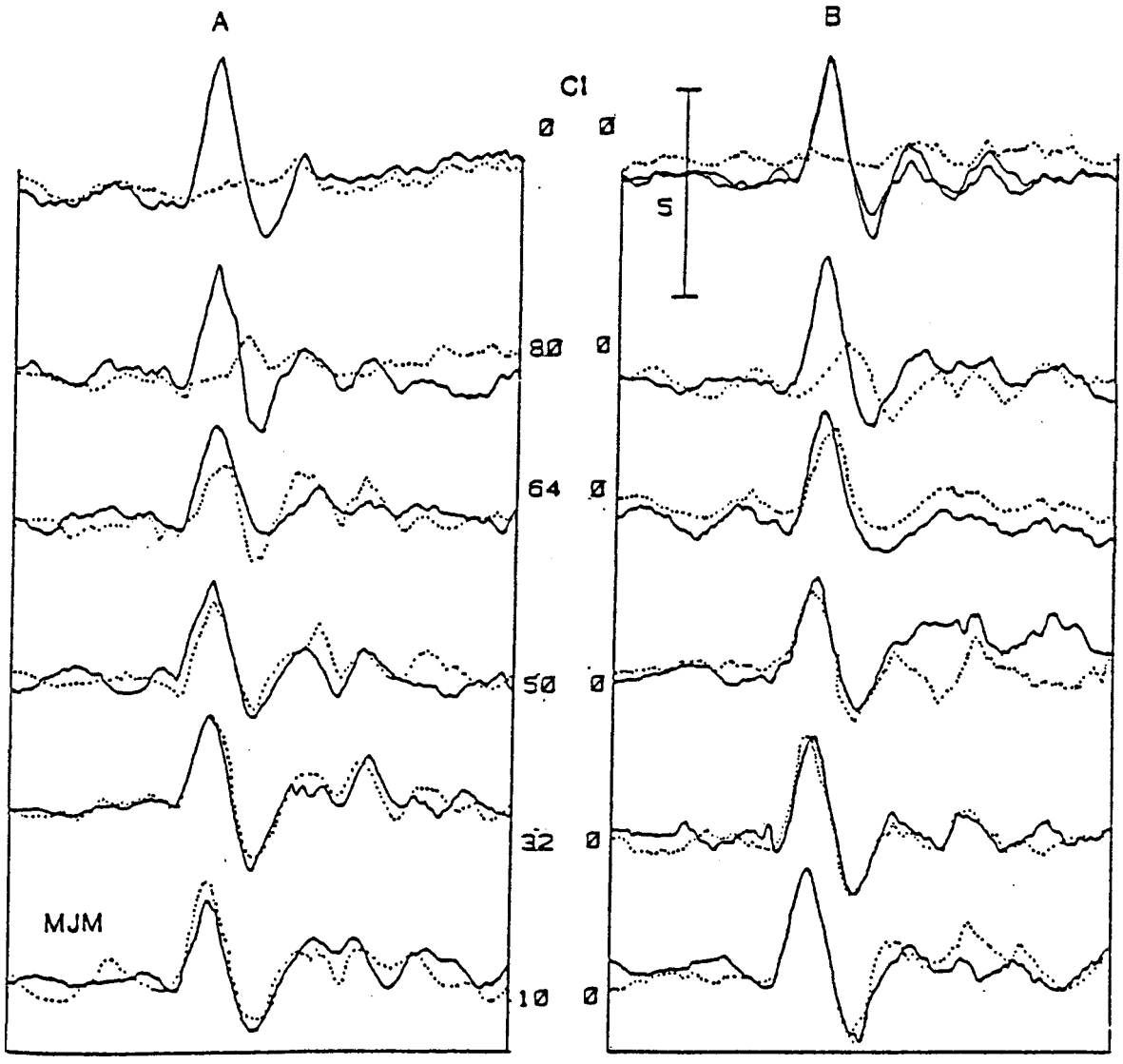


Figure 11.6
VEPs elicited by chromatic and monochromatic square wave gratings.

In column B of figure 11.5b are shown VEPs elicited by patterns of green squares on a red background switched from a yellow blank field. Again there is no minimum for colour contrast VEPs. The control condition in this case was the removal of the red and green filters which were both replaced by yellow ones. In addition, the luminance of the pattern elements was altered by removing a filter of 50 % transmission value. Thus, at the point of former field isoluminance there now existed a contrast difference; minimum contrast was now intermediate between the former position and maximum luminance contrast. This procedure served as a check on the subject's luminance match. At isoluminance clear VEPs are elicited, whilst at the position where formerly the pattern had a contrast of 50% the amplitude of the response is little greater than that of the noise level.

In figure 11.3b the amplitude of CI has been plotted as a function of pattern contrast. The slopes of the functions are similar to those of subject M.J.M and indicate a slight increase in the amplitude of colour contrast VEPs at and around isoluminance.

It has previously been reported that CI can be elicited by square wave gratings and the VEPs illustrated in figure 11.6 indicate that gratings composed of chromatic contrast are equally effective in evoking responses.

11.3. Colour sensitivity of CII.

Results.

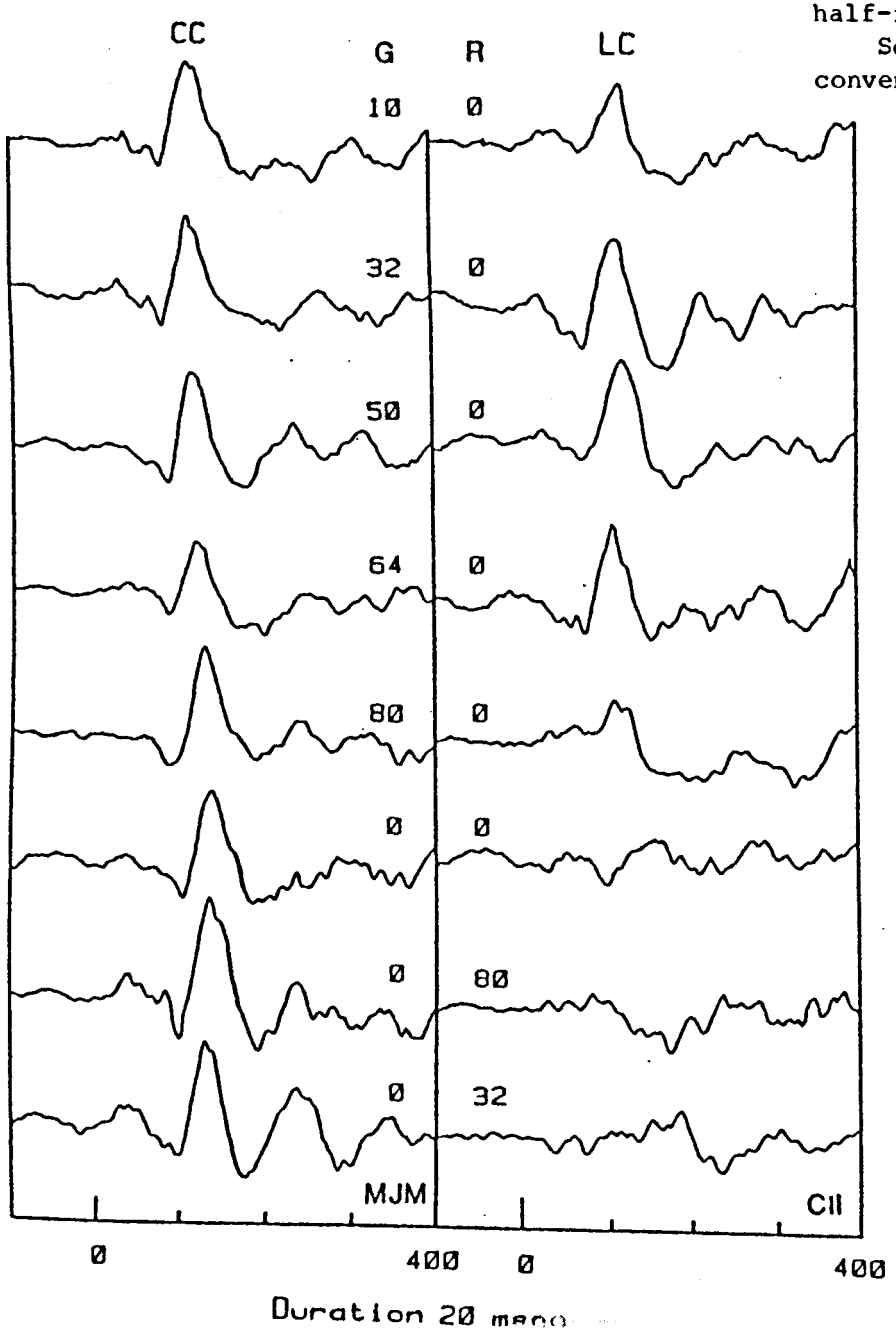
In figure 11.7 are shown, for one subject, VEPs recorded at durations of 20 and 50 msec to the presentation of both chromatic and monochromatic patterns of variable luminance contrast.

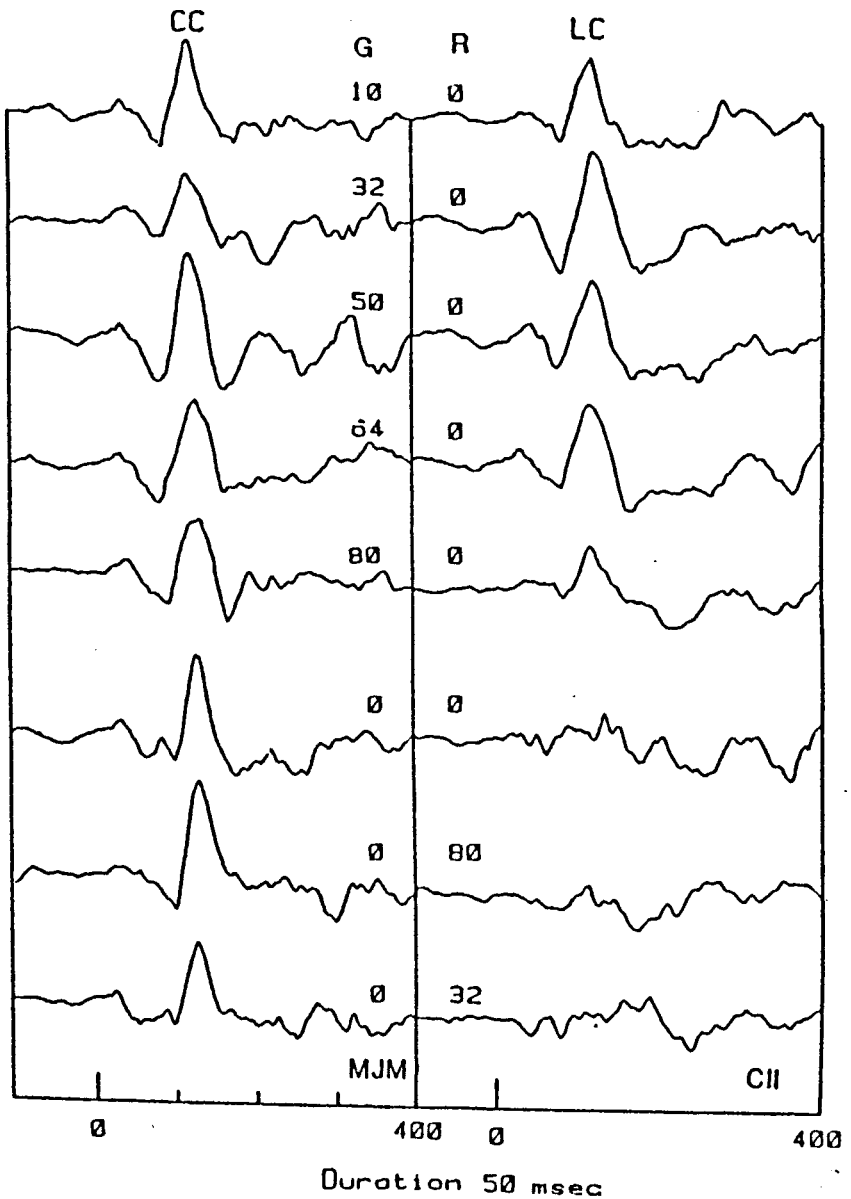
In figure 11.8, the amplitude of CII has been plotted according to the method used in the study of CI reported above. Again for chromatic contrast stimuli, there is no point on contrast scale at which VEP amplitude is reduced to a minimum. This is clearly not the case for monochromatic luminance contrast stimuli, for which a clear minima is evident at the point of red-green isoluminance. The slope of the amplitude v contrast curve for the latter is slightly different from that observed for CI in that it appears to reach saturation level at a lower contrast level. This is in turn consistent with the data of Jeffreys (1977) who has reported that these components saturate at different levels of contrast.

Figure 11.7

Typical form of the response to either colour or luminance contrast patterns. CII component recorded with upper half-field stimulation.

See figure 11.1a for detailed explaination of symbols and convention.





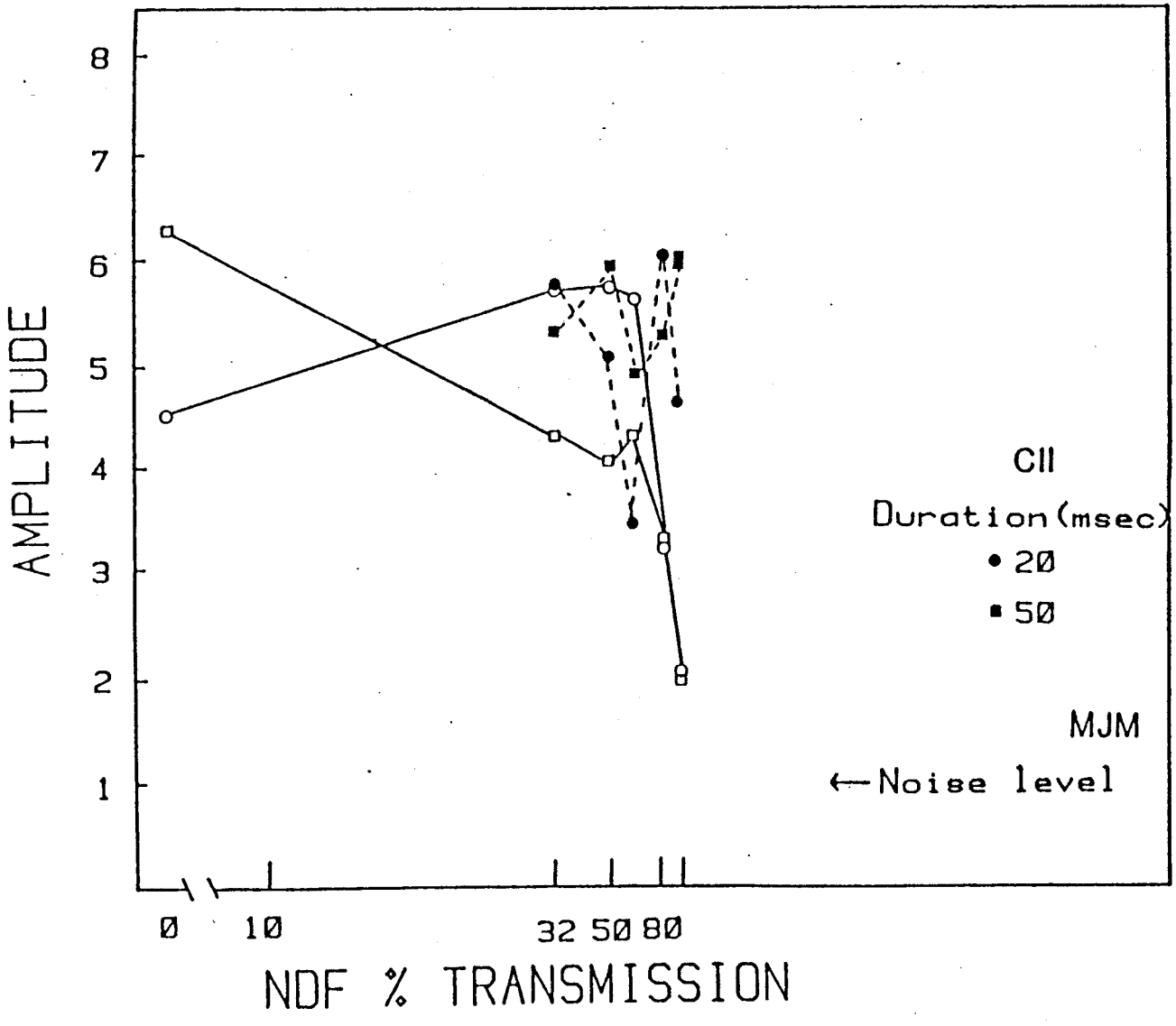


Figure 11.8
Amplitude of CII plotted as a function of element contrast for chromatic and monochromatic luminance contrast stimulation. See text for details.

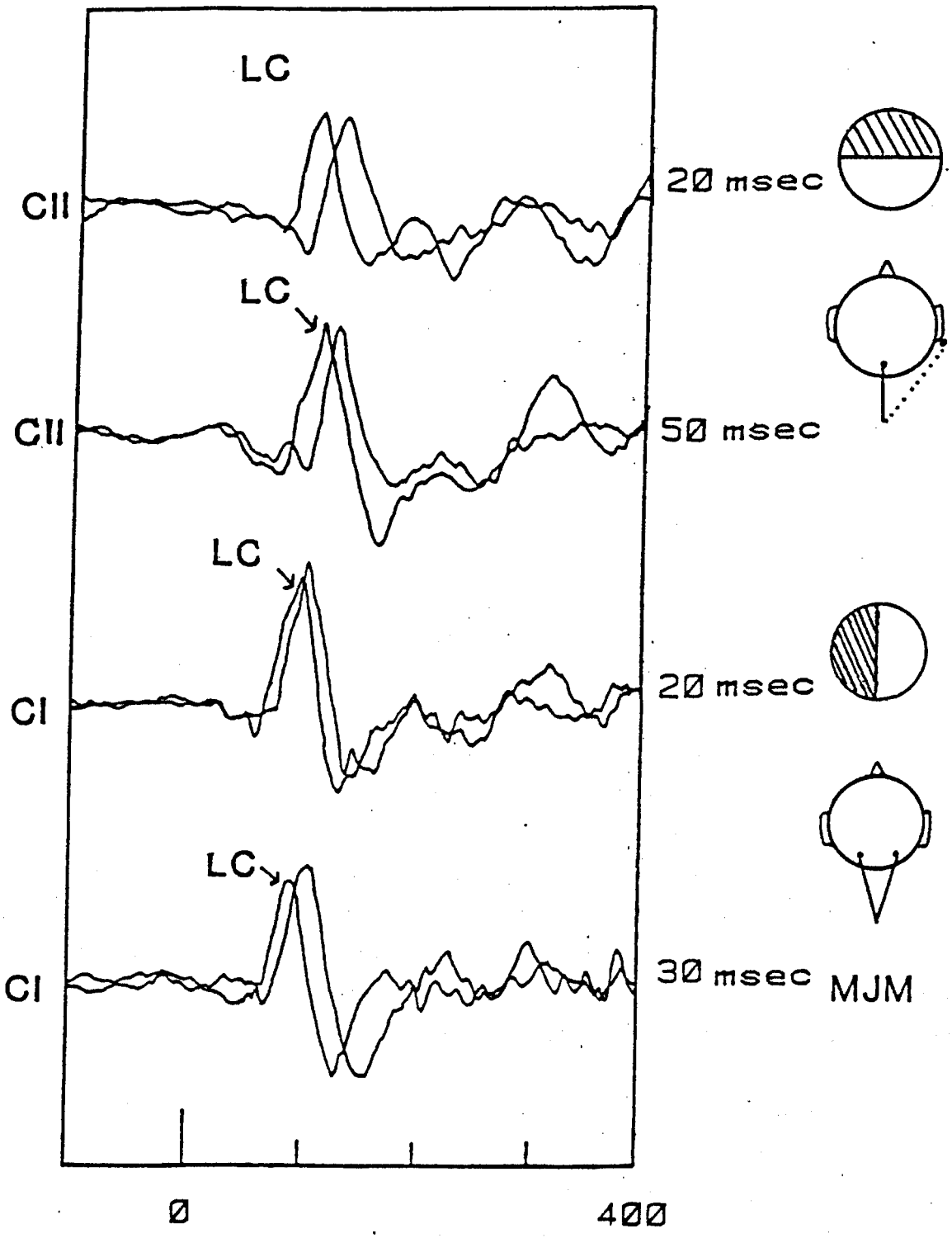


Figure 11.9

Time course of CI and CII elicited by isoluminant colour contrast and maximum luminance contrast stimulation.

The luminance contrast VEP is illustrated by the symbol L.C. and also arrowed. The upper two traces are for CII, the lower for CI. The longer latency VEP is in each case elicited by the isoluminant colour contast pattern.

In figure 11.9 are shown the superimposed CI and CII components elicited by luminance and colour contrast patterns presented at three differing durations. It is evident that there is a 15 to 20 msec difference between the respective components under each condition. The monochromatic luminance VEPs are indicated by an arrow in each case. Since the latency difference between CI and CII under the two conditions is constant the increase in component latency observed for colour contrast VEPs would appear to be of pre-cortical origin.

There is also substantial temporal overlap between the peaks of the two components which suggests a comparable temporal overlap between underlying neural activity within striate and extrastriate cortex. In figure 11.10a are shown for the second subject typical responses under similar conditions, but with lower half-field stimulation. The independence of colour contrast VEPs from overall luminance contrast is again clearly evident.

11.4. Chromatic Aberration

Thus far, the problem of chromatic aberration has not been discussed. Because of ocular chromatic aberration, differently coloured parts of a stimulus pattern would not normally be in sharp focus on the retina. Regan (1973) has argued tha under such conditions luminance contrast VEPs would masquerade as chromatic contrast VEPs. He has shown that under some conditions this is indeed the case. However when chromatic aberration was cancelled by using lenses of the appropriate power, large VEP could still be evoked by isoluminant red/green checkerboards. The results of the previous experiments make it very unlikely that chromatic aberration is a major factor determining the occurrence of VEPs under isoluminant conditions because the properties of the resultant VEP differ markedly between the two main conditions.

The effect of defocusing the stimulus pattern on the CI component elicited by a 150 msec duration stimulus is shown in figure 11.10b for one subject. It is evident that as the retinal image is progressively defocused, the amplitude of the VEP systematically decreases and its latency increases. This suggests, as Gouras and Kruger (1978) found at the single unit level, that chromatic aberration is not a significant factor under these conditions.

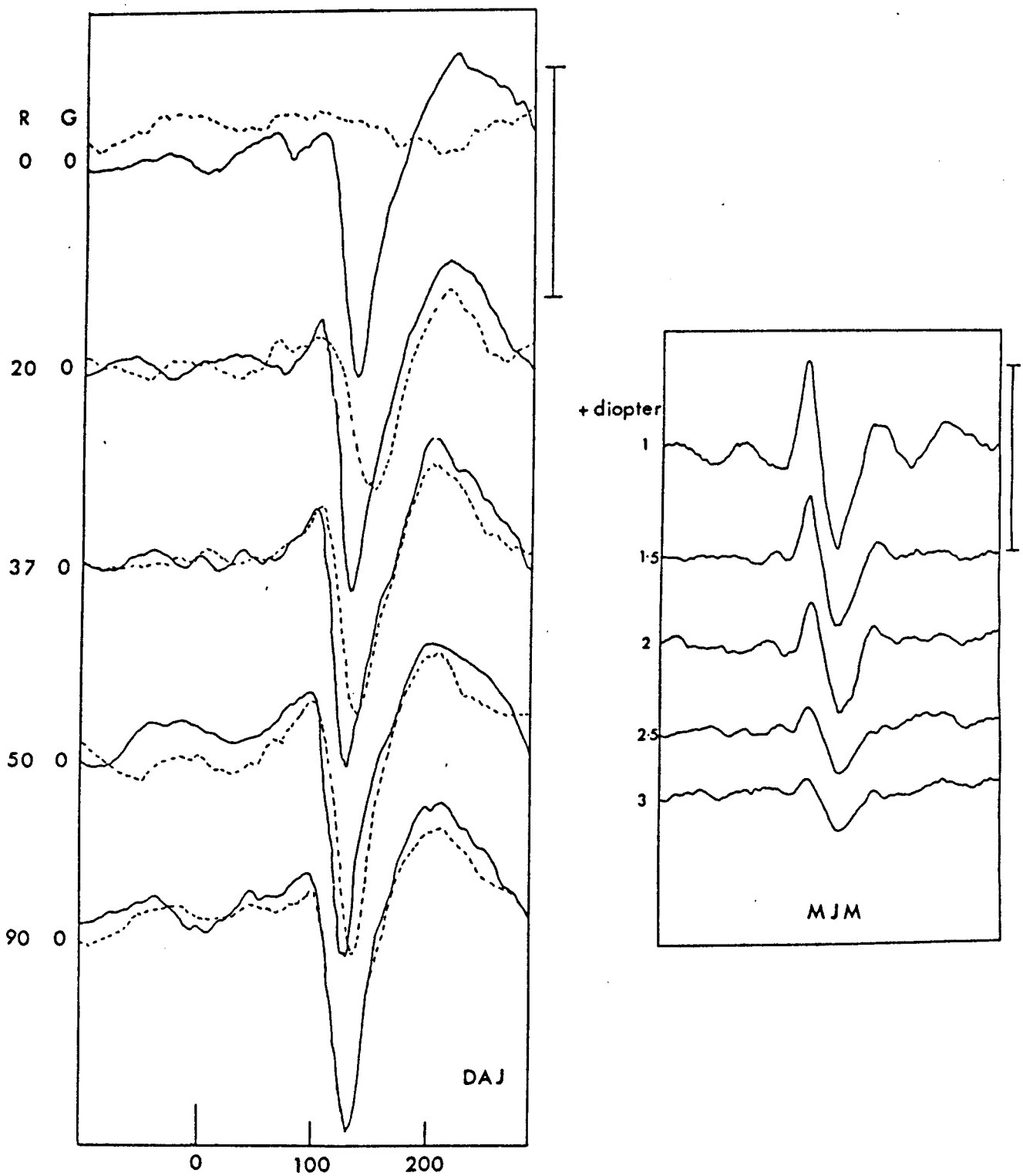


Figure 11.10

A:- CII for subject D.J.A. Full trace is for colour contrast stimulation dashed trace for luminance contrast.

B:- CI elicited by a colour contrast pattern which progressively defocused.

11.5. General Discussion

These experiments have revealed that VEPs specific to pure colour contrast as opposed to luminance contrast can indeed be recorded from the human scalp. The present results question the conclusion reached by Smith (unpublished doctoral thesis, Keele, 1979) that the sources of these components do not contain colour coded cells. In his study, an adaptation paradigm was used to seek evoked potential correlates of colour contingent after-effects. Checkerboard adaptation and test stimuli were used with either red/black or green/black checks, a paradigm that led to four conditions, two heterochromatic (red-green and green-red) and two homochromatic (green-green red-red) adaptation conditions. The results of these experiments did not indicate any differential adaptation under the two conditions.

However Smith's experimental design was not such as to provide evidence in support of either the existence or absence of colour coded cells. His monochromatic stimuli would not be predicted to selectively adapt wavelength sensitive units, (see Gouras & Kruger, 1979). Consider, for example, a simple cell with a vertical orientation preference. Assume that it is presented with a vertical green/black grating optimally orientated within its receptive field and assume further that the receptive field has a green-on, red-off central zone. After the presentation of the above stimulus for some period long enough to produce adaptation, those mechanisms which provide the input to the green-on central region will have become adapted. The unit will now in effect have a red-off central zone and two red suppressive flanks and will thus have momentarily lost its colour contrast sensitivity. It would not however have lost the ability to respond to an optimally orientated stimuli of any other wavelength composition with a luminance difference. A red/black or green/black checkerboard, would still be an effective stimulus since the major adaptation effect would lie in the domain of orientation and spatial frequency, aspects of the receptive field properties that are presumably mediated by complex patterns of inter-cortical wiring. This is indeed exactly what Smith's results show.

If CI does reflect physiological activity within striate cortex, then the present results indicate that many cells within that region are capable of signalling wavelength contrast at isoluminance because the amplitude of the component is as large and in some cases larger for pure colour contrast stimuli than it is for stimuli having maximal

luminance contrast borders. A point that clearly indicates that colour specific VEPs could not be caused solely by luminance contrast alone since, even assuming a significant mismatch between the elements and the background field, it would need to be as much as 0.6 log units. Further evidence that the response obtained to colour contrast cannot be the result of luminance mismatching, is the finding that, whilst the amplitude of the pure colour contrast potential and the maximum luminance contrast potential are similar, their latencies are not.

Chromatic contrast VEPS are therefore independent of relative luminance. From a study of the steady state VEP Regan (1973) also drew the further conclusion that colour signals must still be segregated when they reached the visual cortex. The present results are consistent with this interpretation. However the alternative suggestion that the visual system contains both chromatic and luminance detecting mechanisms is more probable and, given available single unit data, it would appear that luminance and chromatic contrast detecting channels are closely related.

As there is now single unit data from the monkey relevant to our understanding of how colour signals are processed within the cortex an attempt will be made to place the present work within this framework.

Gouras & Kruger (1979) have clearly demonstrated that many cells within the region of foveal striate cortex of the rhesus monkey are responsive to colour contrast in the absence of luminance contrast. Indeed, in spite of having utilised only two parts of the spectrum of the 79 cells studied within that area, about half (38/79,48%) were found to be responsive to successive colour contrast. These same cells, when tested with optimally orientated monochromatic stimuli presented on a white background showed no obvious wavelength sensitivity. Moreover such cells did not appear to show selectivity for the arrangement of the colours defining the chromatic contrast border, and minimal responses were only obtained when the luminance contrast of heterochromatic stimuli was varied.

Other cells were observed which had more selective properties; for these the presence of luminance contrast of whatever polarity failed to elicit unit discharges, but when luminance contrast was minimised and heterochromatic contrast maximised, clear responses were obtained although only for a particular combination and arrangement of chromatic gradient. Such cells can perhaps be considered truly colour specific

and are similar to the population reported by Michael (1978a,b,c,). The important finding of Gouras & Kruger is that information relevant to colour contrast detection reaches a significant proportion of foveal striate cells even though these cells show none of the obvious colour selectivity seen in units within the LGN. This finding is supported by the data of Thorell, Albrecht & DeValois (1978), who report that for sine wave gratings of pure luminance contrast, pure colour contrast or combinations of the two, 85% of a sample of monkey striate cells responded only to both colour and luminance, 10% responded only to luminance contrast and only 1% solely to colour differences.

The properties of the CI component are therefore readily explained by the existence of such cells and the results imply that the human striate cortex contains similar types of cells to that observed in the monkey.

That the CII component is equally as sensitive as CI to patterns of isoluminant colour contrast suggests that the chromatic properties of cells within extrastriate cortex do not differ fundamentally from those in striate cortex. However, it was observed during experiments not reported here that, consistent with the properties of CII observed with achromatic stimuli, square wave gratings of chromatic contrast were ineffective in eliciting this component. The main difference between the properties of these two components appears, even at isoluminance, to be determined by spatial factors.

Teleological considerations would suggest that any mechanism responsive to visual contours should be as sensitive to these contours whether they are produced by chromatic or luminance variations. Psychophysical data would support such a conclusion (see Boynton,1979). The finding that cortical cells can 'signal' wavelength differences at isoluminance has been considered something of a mystery, as these same cells appear to have no chromatic specificity, (see Boynton,1979). The ability to make refined hue judgements seems unlikely to be mediated by cells of this type. Their role in visual perception may be to make 'form' detection independent of luminance contrast.

A possible explanation of the latency differences between VEPs elicited by maximal luminance and isoluminant colour contrast patterns is given in section 11.7 where the temporal properties of the VEP elicited by these types of stimuli are studied in some detail, they would, however, appear consistent with the small latency to discharge differences which have been reported for tonic and phasic cells in

monkey visual pathway (Gouras,1969).

11.6 Temporal resolution of colour and luminance contrast patterns

Human psychophysical data suggest that there are differences in the temporal and spatial processing of colour and luminance contrast stimuli. Specifically, chromatic CFF has been shown to be poorer than luminance CFF (see Boynton,1978), this being particularly true for short wavelength stimuli, presumed to optimally stimulate the so called Blue cone mechanism. A further difference has been reported between the integration time constant of the so called chromatic and luminance system (Regan & Tyler,1971; Krauskopf & Mollen, 1971). The evidence suggests different integration time constants for the three cone mechanisms, all of which are longer than that of the luminance system.

Single cell recordings from the retina support the psychophysical data in showing that ganglion cells have a higher temporal cut off for luminance than for chromatic flicker (Zrenner & Gouras,1980; Gouras & Zrenner,1979). This pattern is repeated at the level of the LGN where Gielen & Ginsberg (1980) report that 'X' type cells in the monkey LGN have higher frequency cut-off and lower low frequency cut-off, for chromatic than for achromatic stimuli. The evidence points to wavelength-dependent differences in the temporal properties of the system, and physiological data suggests that these differences occur at a very low level of processing. They should therefore be evident in the response of the CI to stimuli differing in either chromatic and luminance contrast.

Procedure

The stimuli were similar to those used in the preceding experiments. In this case, brief pairs of patterns each of 20 msec duration were presented to the left half-field (1.5 degree).

For the colour contrast condition the patterned field consisted of green squares on a red surround which alternated with a blank red field of the same overall mean luminance (the luminance of all fields were again matched by heterochromatic photometry at 12 Hz). For the luminance contrast condition, the green field was occluded, thus producing a pattern of black squares on a red surround. Seven runs of 8

sweeps were undertaken at each randomly determined SOA. The limit of temporal resolution for brief discrete pairs was compared to that obained with high frequency pattern-onset stimulation with both luminance and colour contrast stimuli. The method employed was similar to that used in chapter 6. Two subject were used in the study of resolution for brief pairs and one in the study of high frequency pattern-onset.

Results

The waveforms shown in figure 11.11 indicate the form of the response obtained for both subjects under these conditions. The dashed trace is for the luminance condition, the full trace for the isoluminant colour contrast. Several features are evident. Firstly the amplitude of the potential to colour contrast stimuli is greater than that to luminance contrast under the same conditions. Secondly, although the amplitudes of the colour contrast VEPs are larger, their latencies are longer. For subject MJM, the peak latency of the colour contrast VEPs is 100-103 msec whilst that to the maximal luminace stimuli is between 90-92 msec at this level of background luminance. A similar pattern is evident for HD: the overall peak latency of CI being for this subject approximately 3-5 msec longer than that for MJM. The results therefore replicate the findings and support the conclusions of the VEP experiments reported above.

The main finding of this experiment, however is that the limit of temporal resolution for the CI component is longer for the colour contrast stimuli than it is for the maximal luminance contrast stimuli. For luminance contrast, the resolution limit appears to be approximately 50-60 msec SOA for subject MJM and 70-80 msec for subject HD. For chromatic contrast however limiting resolution appears to be at 75-85 msec for subject MJM, and 90-100 msec SOA for subject HD. The limit of resolution for both subjects in the luminance contrast conditions is slightly longer than that observed for both subjects in experiment 1 of chapter 4 of this thesis. This may be due to several factors: Firstly, background luminance in the present case is lower than that used in those experiments. This is perhaps contradictory to the previous finding that background luminance had little effect on the limit of temporal resolution for achromatic dot stimuli. The present stimuli were not however achromatic and this may have resulted in the selective stimulation of specific cone mechanisms which are thought to have longer time constants than that of the so called luminance system.

Figure 11.11

Ilustrates the VEPs elicited under double pulse stimulation for colour and luminance contrast conditions. For MJM the colour contrats VEPs are shown in the dotted trace, for subject HD they are shown in the full trace.

See text for discussion.

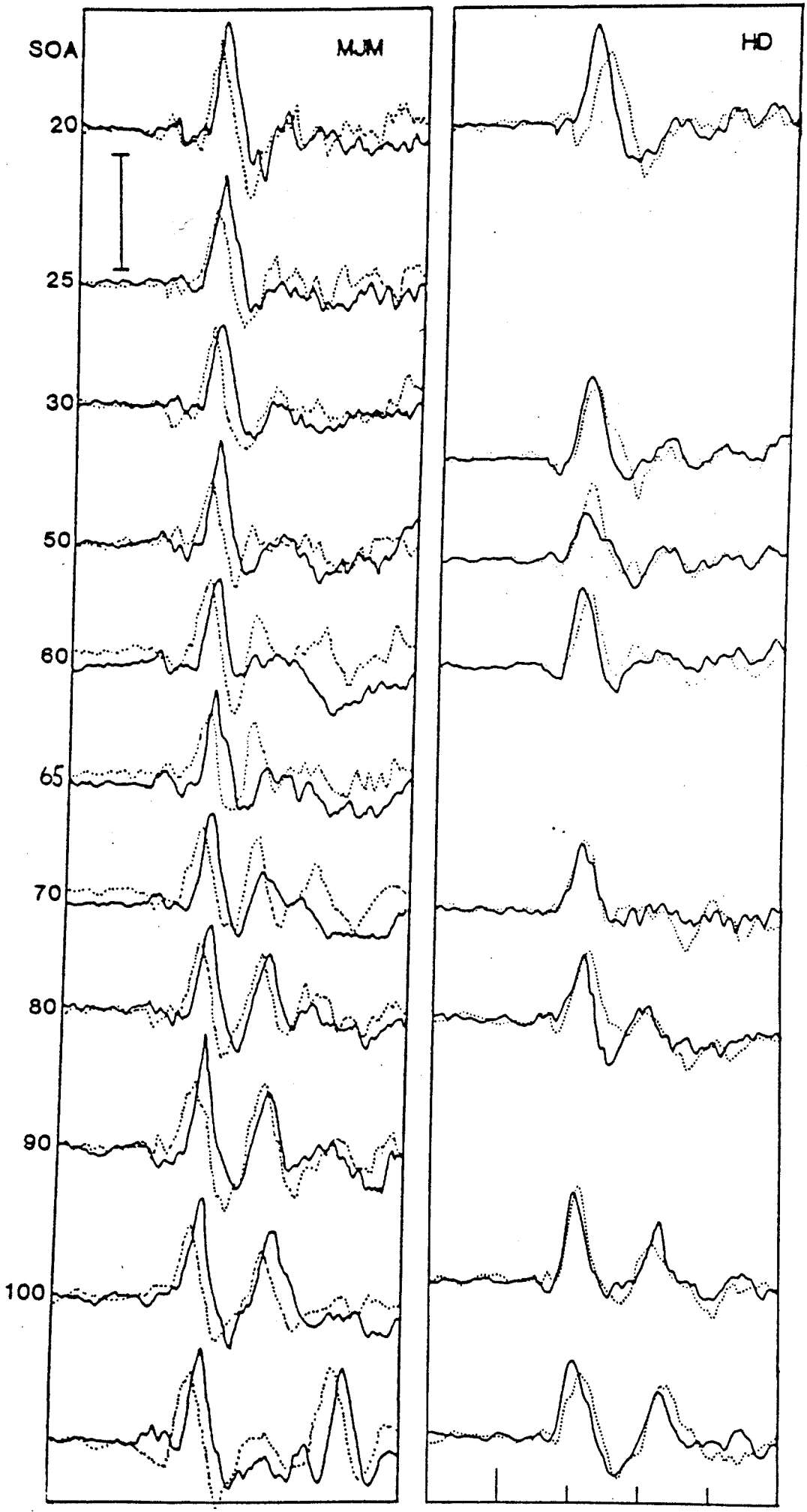


Figure 11.11

Ilustrates the VEPs elicited under double pulse stimulation for colour and luminance contrast conditions.
See text for discussion

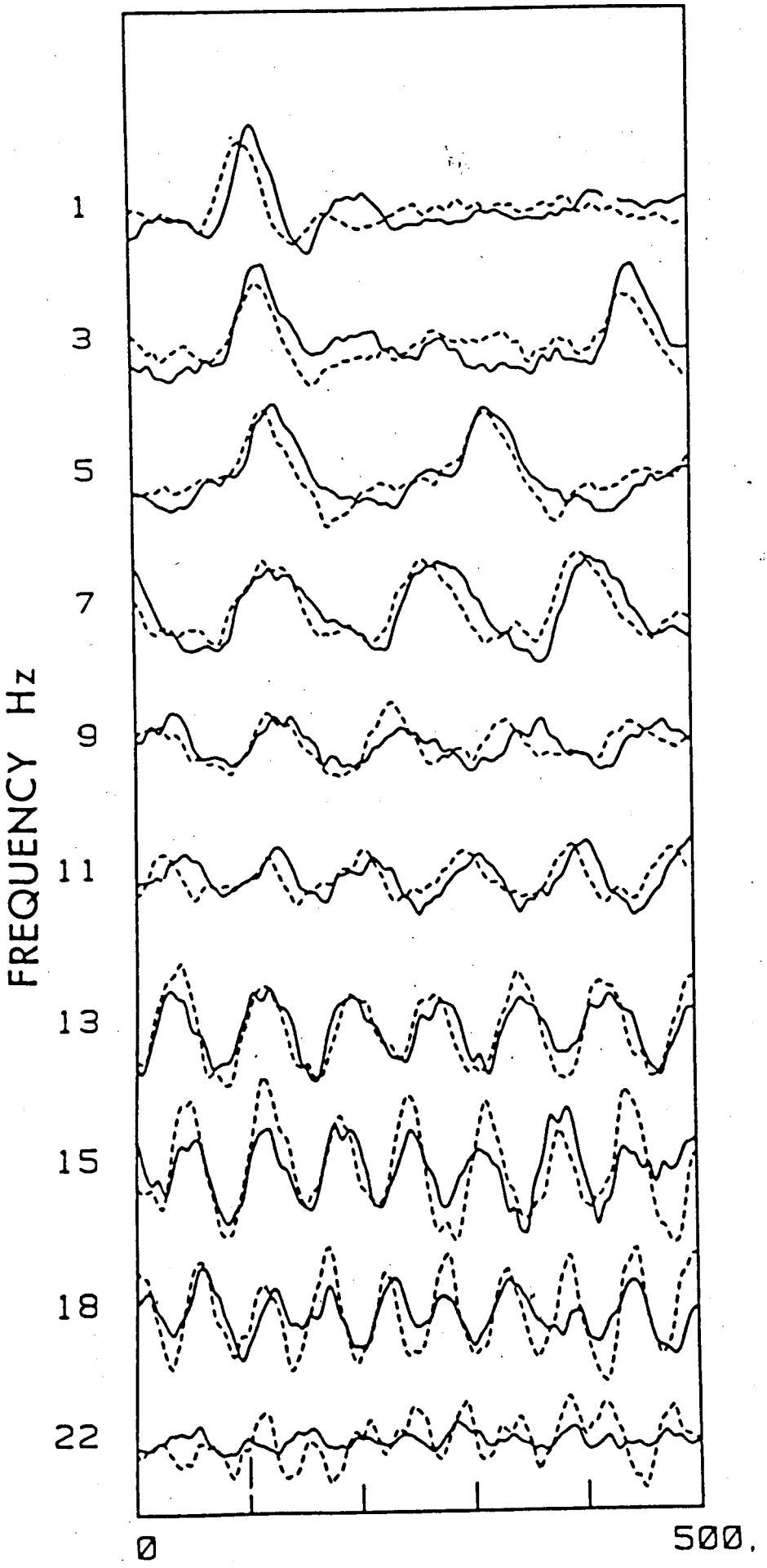


Figure 11.12
High frequency VEP's elicited by colour contrast (full trace) or luminance contrast (dashed trace).

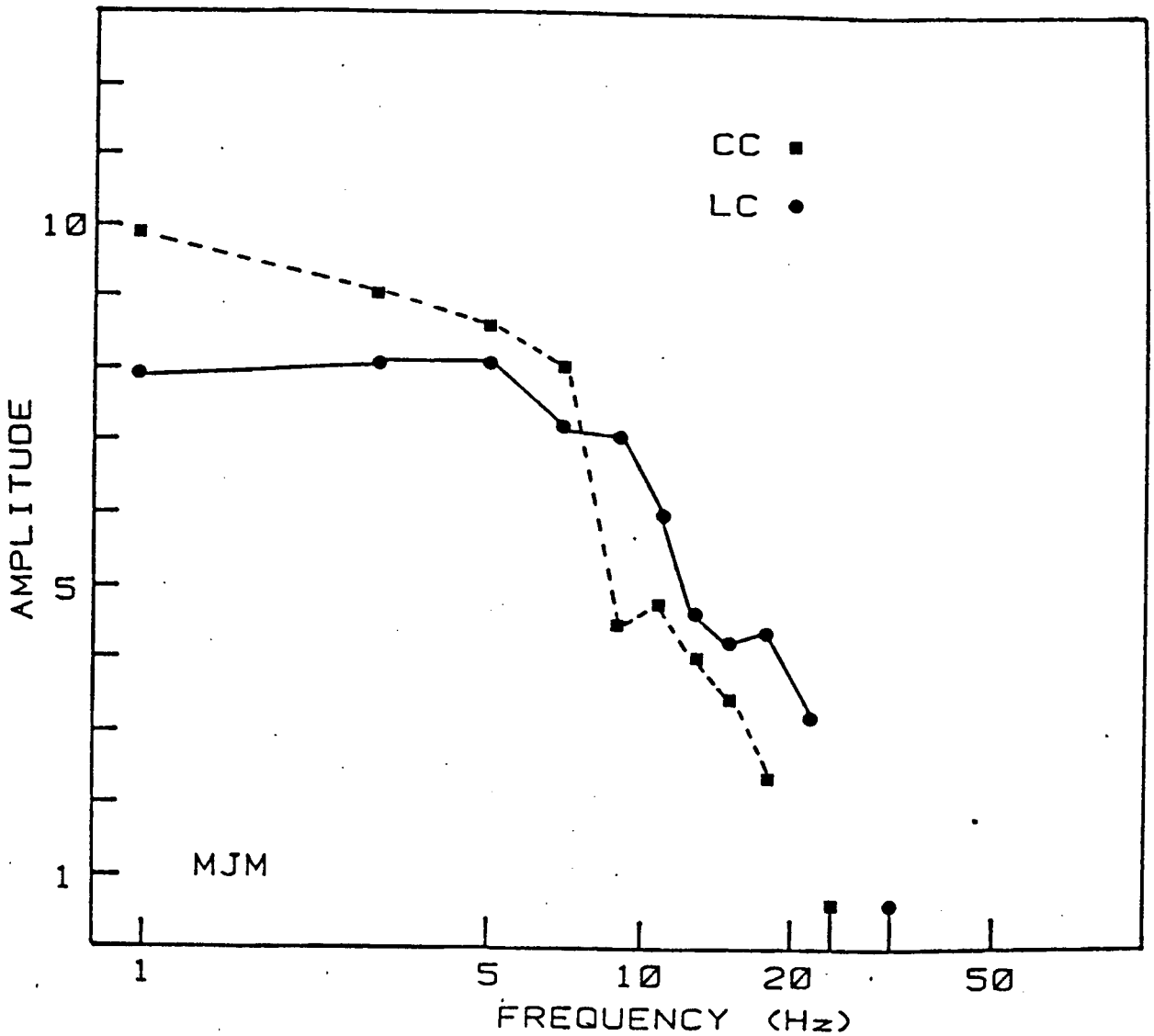


Figure 11.13

Plots of peak-to-peak amplitude of steady state VEPs as a function of the temporal frequency of stimulation.

Colour contrast data are indicated by the dashed line, luminance contrast by the continuous line.

Symbols on the abcissa mark the psychophysically determined CFF under the two conditions. Data for one subject.

Secondly, a small field 1.5 degree has been used. It is thus possible that a combination of the above factors has resulted in the increased limit of component resolution observed in the present case.

In figure 11.12 are shown the waveforms produced by chromatic and luminance pattern flicker. In figure 11.13, the mean peak-to-peak amplitude of these VEPs are plotted as a function of temporal frequency. The waveforms indicate the latency difference of the VEPs evoked by the two types of stimulation even at medium temporal frequencies. Consistent with the reported psychophysical data, CFF for colour contrast VEPs is lower than that of the luminance contrast VEPs. The slope of the VEP amplitude function extrapolates to the psychophysically determined CFF. At low temporal frequencies the amplitude of the colour contrast VEP is greater than that of luminance contrast. The results are therefore in agreement with the previous data for brief discrete pairs in showing that at the electrophysiological level temporal processing of isoluminant colour contrast is poorer than that of luminance contrast.

11.7. Discussion

The VEP data substantiates both psychophysical and physiological findings which suggest that those 'mechanisms' processing temporal changes in wavelength have a lower high frequency cut-off than those 'mechanisms' processing luminance variations (Boynton,1979, Kelly,1975). The present VEP data cannot be accounted for by a decreased effectiveness of coloured contrast patterns in eliciting neural activity because, at low temporal frequencies, they evoke larger VEPs. The decrease sensitivity of the VEP to the presentation of colour contrast patterns at high temporal frequencies must therefore be due to temporal factors.

Although psychophysical studies of temporal resolution for brief discrete pairs of colour contrast patterns are not available, comparable investigations of CFF for so-called 'colour' mechanisms suggest that all have greater high frequency and smaller low frequency cut off than the so-called 'luminance' channel. This is supported by the VEPs recorded under steady-state conditions.

Both results for brief discrete pairs and steady state stimulation probably share a common mechanism, of fairly low physiological level. Zrenner & Gouras (1980) have reported that at high flicker rates the

chromatic antagonism of colour opponent ganglion cells changes to synergism of the centre and surround mechanisms. This has been shown to considerably improve the response to high frequency luminance flicker (Gouras & Zrenner,1979). A similar mechanism may account for the greater temporal resolution of those mechanisms processing luminance contrast in the striate cortex.

A possible explanation of both the longer latency of CI to colour as opposed to luminance contrast, and the better temporal resolution of the latter relative to the former under both steady-state and transient conditions, may be related to the properties of the Phasic and Tonic cell class. The tonic class have colour-opponent receptive fields (Gouras,1970) whilst the phasic class do not. The tonic class have small receptive fields, are fed by smaller axons and have been reported to have a longer discharge latency, of some 10-15 msec, (Shiller & Malpelli,1978) than the 'broad band' phasic class. If the the phasic class were to be optimally stimulated by isoluminant colour contrast stimuli, then this may explain the longer latency of CI and its poorer temporal resolution under these conditions.

Chapter 12:- Colour mapping studies

Introduction

It was shown in chapter 11 that the generators of both the CI and CII components were equally sensitive to both colour and luminance contrast. Zeki (1974; 1978d; 1980) however has reported a predominance of colour coded cells in an area of extrastriate cortex, called by him V4, which far outweighs any other receptive field preference. Zeki's data suggests that there are two main afferent projections to V4. The first projection is from that region of V1 in which colour selective cells are most densely populated. This projection is reported to feed only a limit part of V4. The second projection is an indirect one from V1 through V2 onto that region of V4 to which receives the direct project from V1 (Zeki,1977; 1978). The fact that the region of V1 which projects directly to V4 has a high concentration of wavelength selective cells cannot, of itself, explain the wavelength preference of cells in V4, since the size of receptive fields within the latter are larger than would be predicted on the basis of the direct input from V1. Indeed they are similar to those found in V2. This suggests that the properties of receptive fields within V4 are determined by input from V2, although Zeki's data suggests that this area has few colour selective cells

Gouras & Kruger (1979) have shown that this is not the case, and thus the higher selectivity of V4 cells for colour, would therefore appear less mysterious; they may reflect a reorganisation of input from the two pathways which traverse regions known to contain cells responsive to wavelength differences.

Thus we have a region within monkey visual cortex reported to have a high concentration of colour selective cells. In this chapter a series of experiments are reported in which the VEPs elicited by patterns of luminance and colour contrast are recorded from a multiple array of electrodes. The aim of this study is twofold.

A:- to search for new VEP components specific to colour contrast stimuli and, if found, to compare their distributions with those of the pattern specific components CI and CII.

B:- to compare the relative distribution of the known pattern specific components elicited by colour and luminance contrast stimuli,

to determine whether the introduction of 'colour' produces any changes in the scalp topography of these components.

Zeki's (1978a,d) has suggested that the representation of the visual field within V4 reveals a further feature distinguishing it from other extrastriate visual areas, because receptive fields appear to be arranged in a non-retinotopic manner. There is perhaps an inherent contradiction in this statement because a 'functional' visual area is distinguished, at least by Zeki (1978a), on the basis of a retinotopic organisation of receptive fields within a restricted cortical space, which otherwise indicate no anatomical or cytoarchitectral differences from the surrounding cortex. It is thus possible that the so-called area V4 is little more than a series of isolated patches of visual field representation rather than a distinct functional entitity in which the previous principles of visual field mapping do not hold. At present this question has not been adequately resolved and and it will be left to further single unit and degeneration studies to clarify the issue.

Given the gross similarity between visual function in monkeys (rhesus) and man, it might be predicted that in human visual cortex there will exist a functional visual region comparable to V4. Previous VEP studies have not examined in detail the distribution of activity evoked by colour contrast patterns, although Clynes & Kohn (1967) have reported experiments in which coloured stimuli were found to produce a slightly different distribution of scalp activity from that of achromatic ones. It is difficult to compare Clynes & Kohn's results with those pattern specific components identified by Jeffreys and Axford (1972a,b) because of procedural differences. However the components identified by them do have similar time courses and source polarity to those reported by Jeffreys and Axford.

If there is an area of visual cortex which, as Zeki's data (1978a) suggests, has a very high proportion of colour specific cells, then it is possible that the analogous area in man would, when the appropriate stimulus conditions are found, give rise to activity not evident with achromatic pattern apparence. The difficulty here however is that if, as Zeki's data suggests, V4 has non-retinotopic organisation, then the principal method by which VEP components of visual cortical origin can be distinguished, i.e., their dependence on pattern location, will be ineffective because, even with achromatic pattern appearance or with an overall change in mean luminance in the absence of pattern, non-pattern

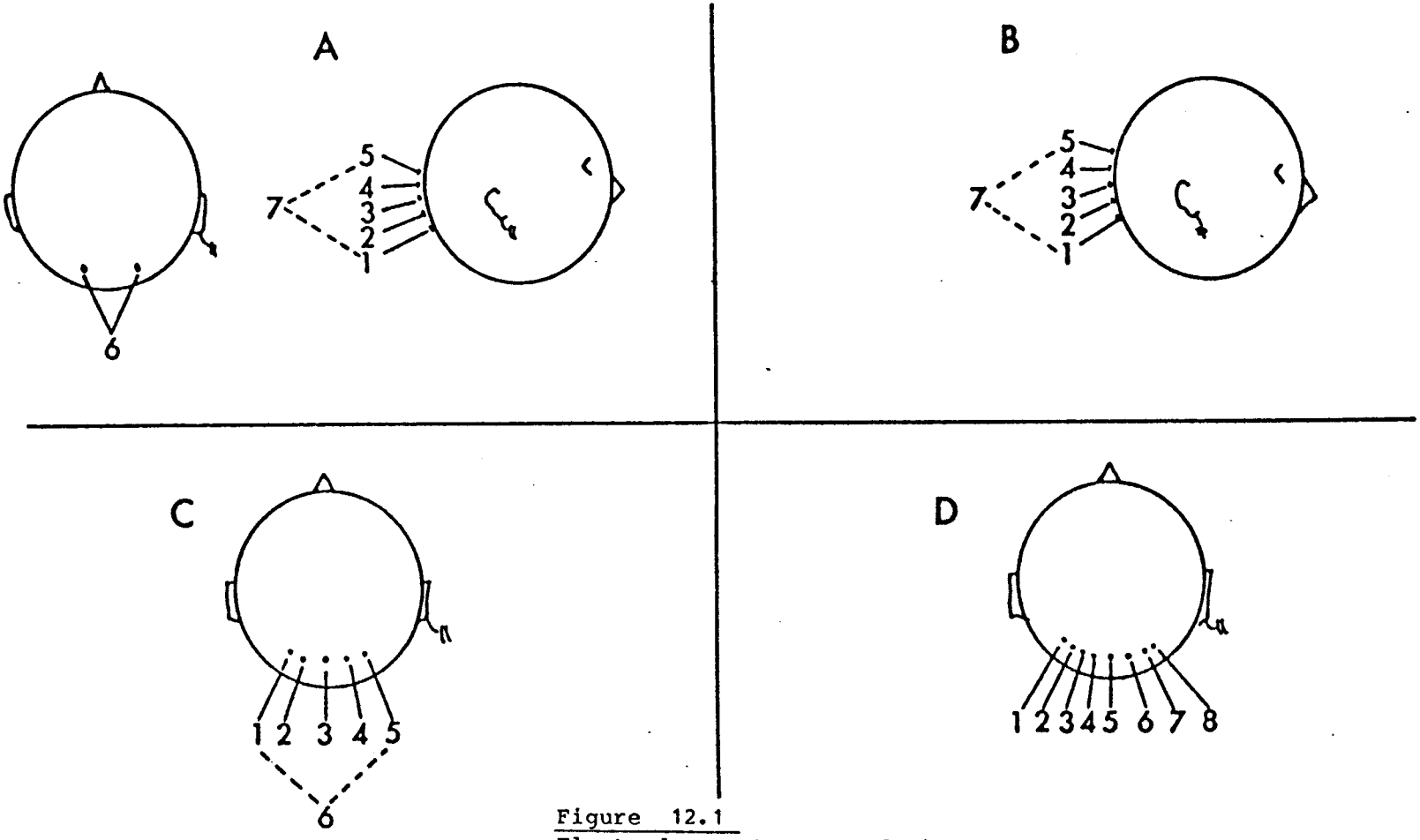


Figure 12.1

Electrode montage used in experiments 1 to 4 of this chapter. Electrode seperation is 2.5 cm in each case. Transverse electrode arrays are 4cm above the inion. Monopolar electrodes are referenced to the right ear.

A:- for experiment 1

B:- for experiment 2

C:- for experiment 3

D:- for experiment 4

specific potentials can be observed, (see Jeffreys,1977; and Jeffreys & Musselwhite (in prep).

However, some of these non-pattern specific components have an asymmetric transverse disribution, which might be consistent with their generation in an area of visual cortex in which the principle of retinotopic organisation does not apply.

The major non-pattern specific VEP is the N150 component which can be recorded in most subjects. Given the position of V4, in terms of afferent input from V1, it would be predicted that any activity evoked in such a region would succeed, that of CII. The peak latency of CII in the experiments of chapter 11 was some 115-125 msec for isoluminant colour contrast patterns and the latency difference between CI and CII some 15-20 msec. Assuming a similar latency difference between activity at the cortical generator of CII and that of the region in which the functional area V4 is located it is probable that activity from the latter would overlap temporally with that of the non-pattern specific component N150. The predicted absence of polarity reversal resulting from activity within a non-retinotopically organised visual area would make the identification of colour specific VEP components difficult.

Alternatively, the assumption that there would be a component of different scalp distribution to that of the already identified components may be misplaced. Activity within this postulated 'colour' area may overlap temporally with that of CII, given the close proximity of the visual areas within extrastriate cortex. If this is the case then the only way to determine whether activity was originating from a region of visual cortex other than that producing contrast specific responses would be to determine the relative differences in amplitude of the VEP as a function of electrode location and stimulus conditions.

12.1:-Longitudinal mapping: Subject 1.

Procedure

The electrode positions used in this study are shown in figure 12.1a. Each electrode is 2.5 cm apart and situated on the midline. In addition the standard bipolar electrode positions were used to record CI (position 6). This was done to provide a reference point from which subsequent activity could be compared. A further bipolar derivation similar to that used by Spekreijse et al (1977) was used. This was

recorded between electrode position 1 and 5, and referred to as electrode position 7. Calibration pulses of 10 μv amplitude are shown in figure 12.1b. These refer to all subsequent experiments of this chapter.

Results

Data from these multielectrode studies are detailed, and it is not easy to represent them in concise manner. It is for this reason that the waveforms in each of the conditions of this experiment have been shown in figures 12.2 a-g to indicate the consistency of the responses over experimental conditions.

In figures 12.2a & b are shown responses elicited by stimulation of the upper and lower fields. The electrode positions at the right of each figure correspond to the positions shown in figure 12.1. Columns A, B, C and D refer to the following conditions:-

A:- achromatic luminance contrast

B:- monochromatic luminance contrast

C:- isoluminant colour contrast

D:- isoluminant colour contrast + 80% neutral density filter in the green (pattern element) field.

It is evident that for upper half-field stimulation the waveforms at electrodes 1-5 are dominated by a large positive potential the peak latency of which is shorter for condition A than B and C. The latency differences are small but amount to some 10-15 msec from A-C.

In the lower half-field VEPs, recorded from the monopolar electrodes 1-5, there is a large negative peak of similar latency to that of the positive peak recorded in the upper half-field. This negative activity is maximal at posterior electrodes in contrast to that of the positive peak in the upper half-field responses which are maximal at the anterior electrodes.

In the lower half-field waveforms recorded from electrode position 6, there is a large positive potential, the latency of which increases from condition A-C. This peak is CI, which for this subject, reflects activity within that region of the striate cortex representing the lower left quadrant. At electrode position 7, there is evidence of a large negative

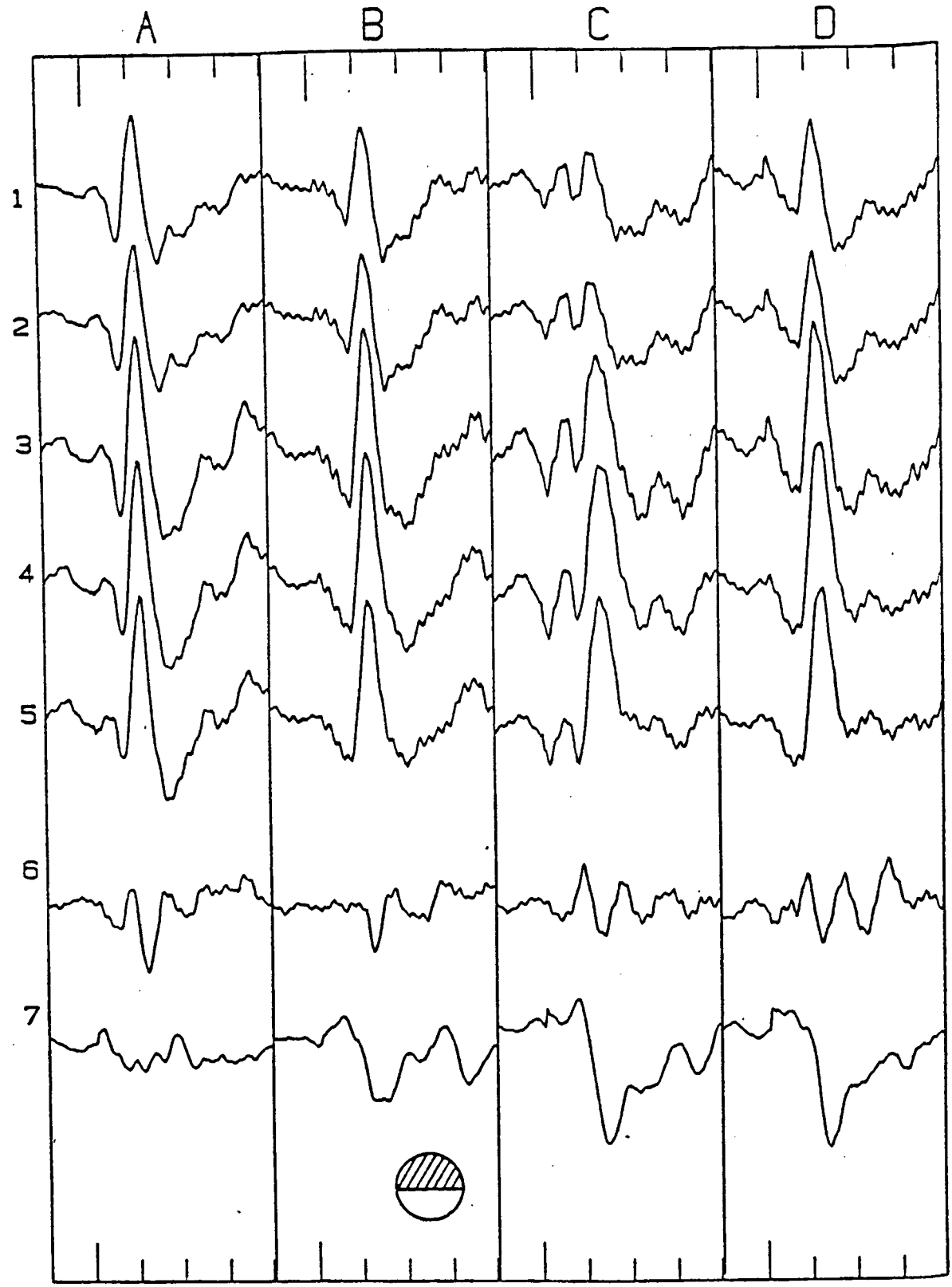


Figure 12.2 Fig. 12.2a

Waveforms recorded as a function of pattern location, under each of the four types of stimulus conditions used in experiment 12.1.

Columns A-D indicate the four types of stimulus patterns described in the text.

Numbers 1-7 refer to electrode locations, see figure 12.1. A 500 msec sample of the waveform has been shown in each case. One division equals 100 msec. The stimulus is presented after 100 msec.

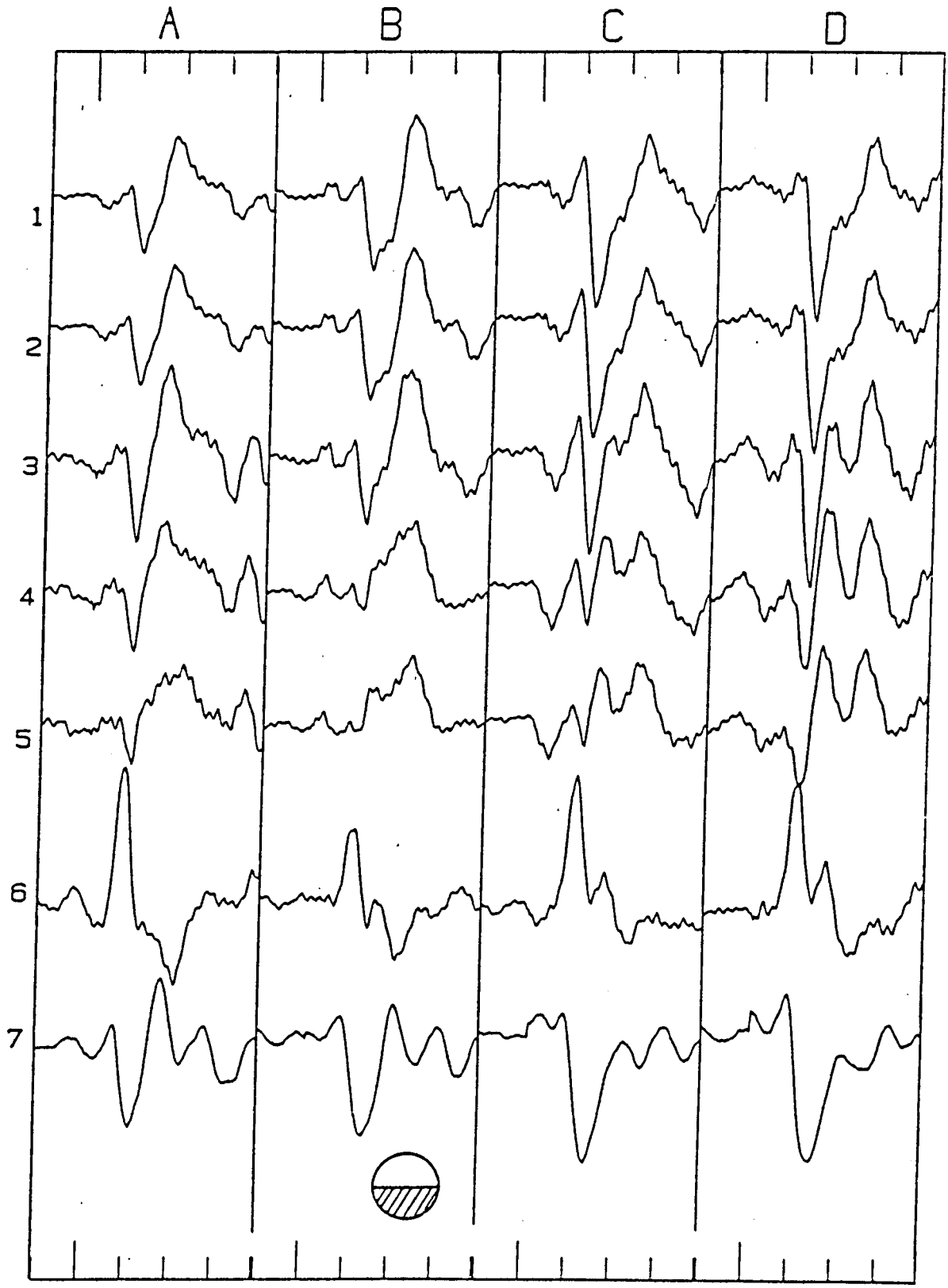


Fig. 12.2b

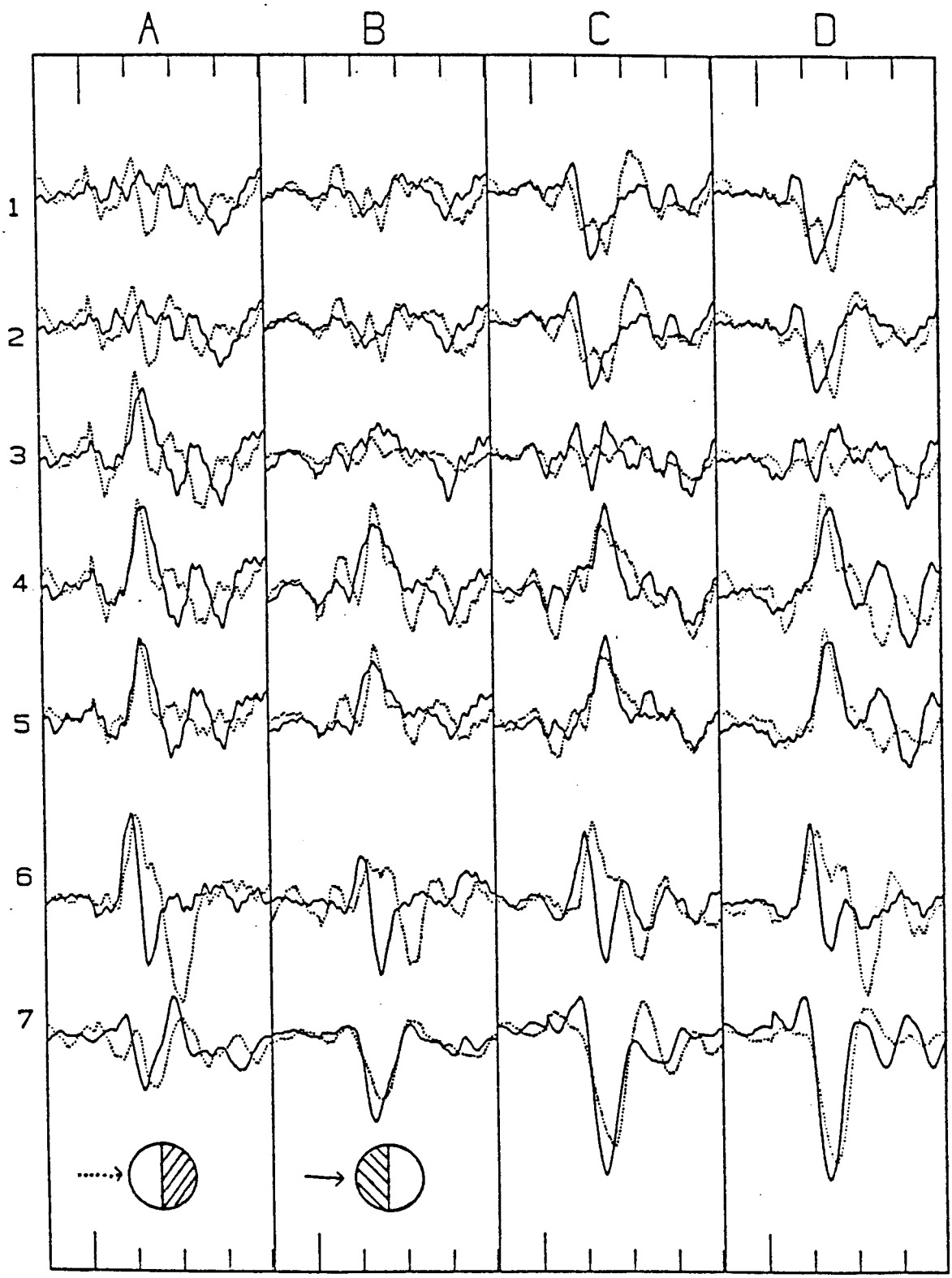


Fig. 12.2c

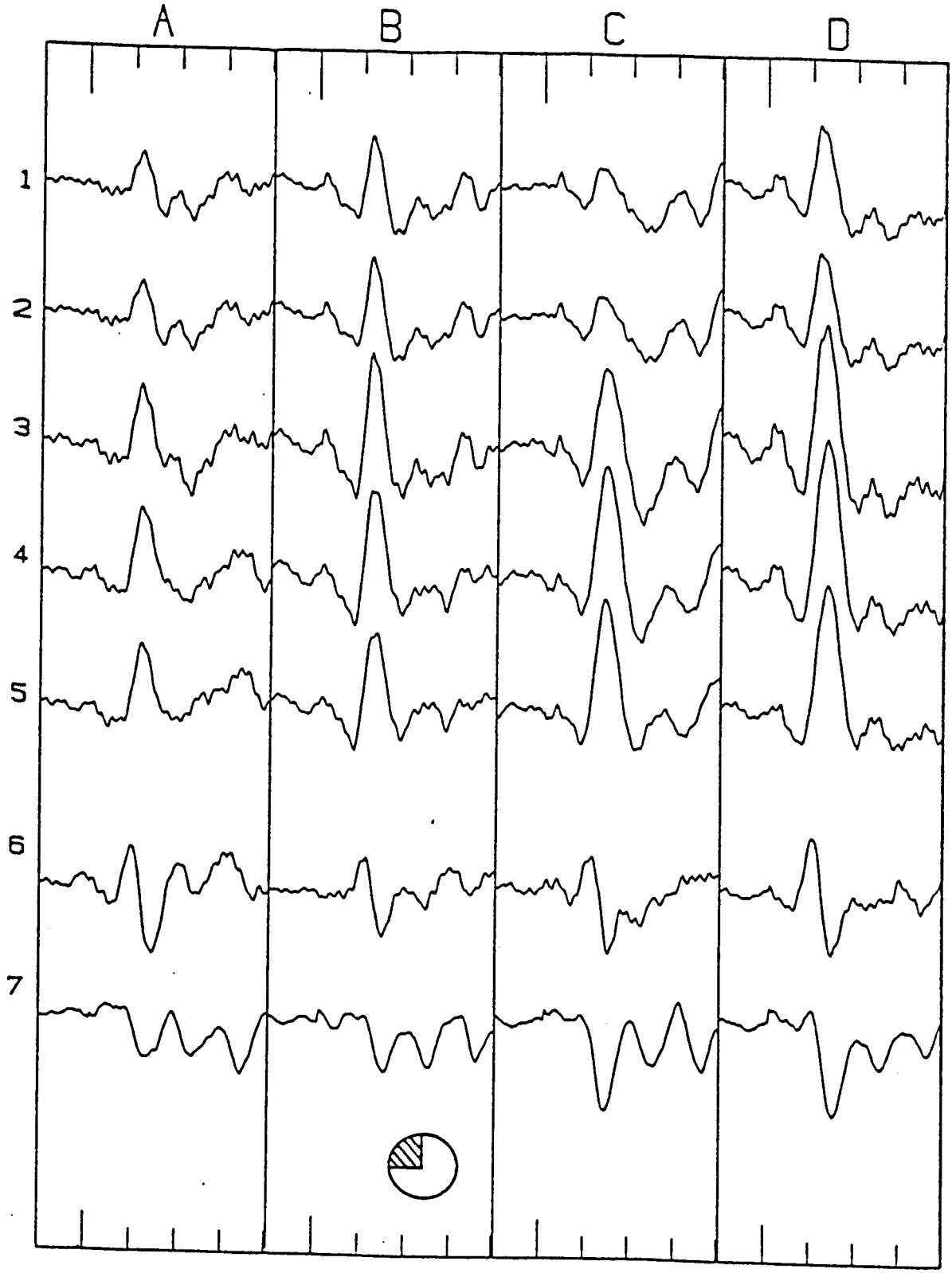


Fig. 12.2d

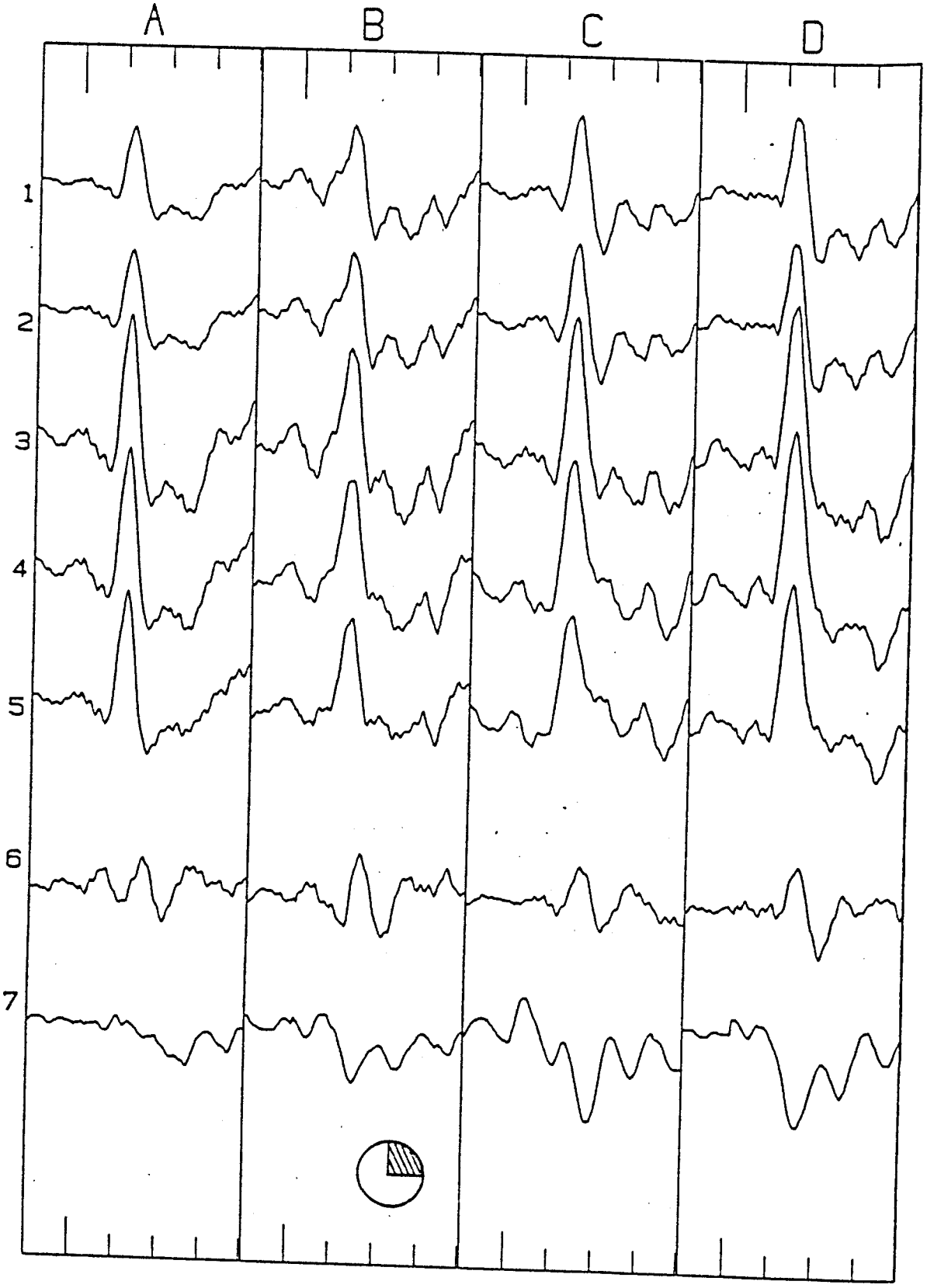


Fig. 12.2e

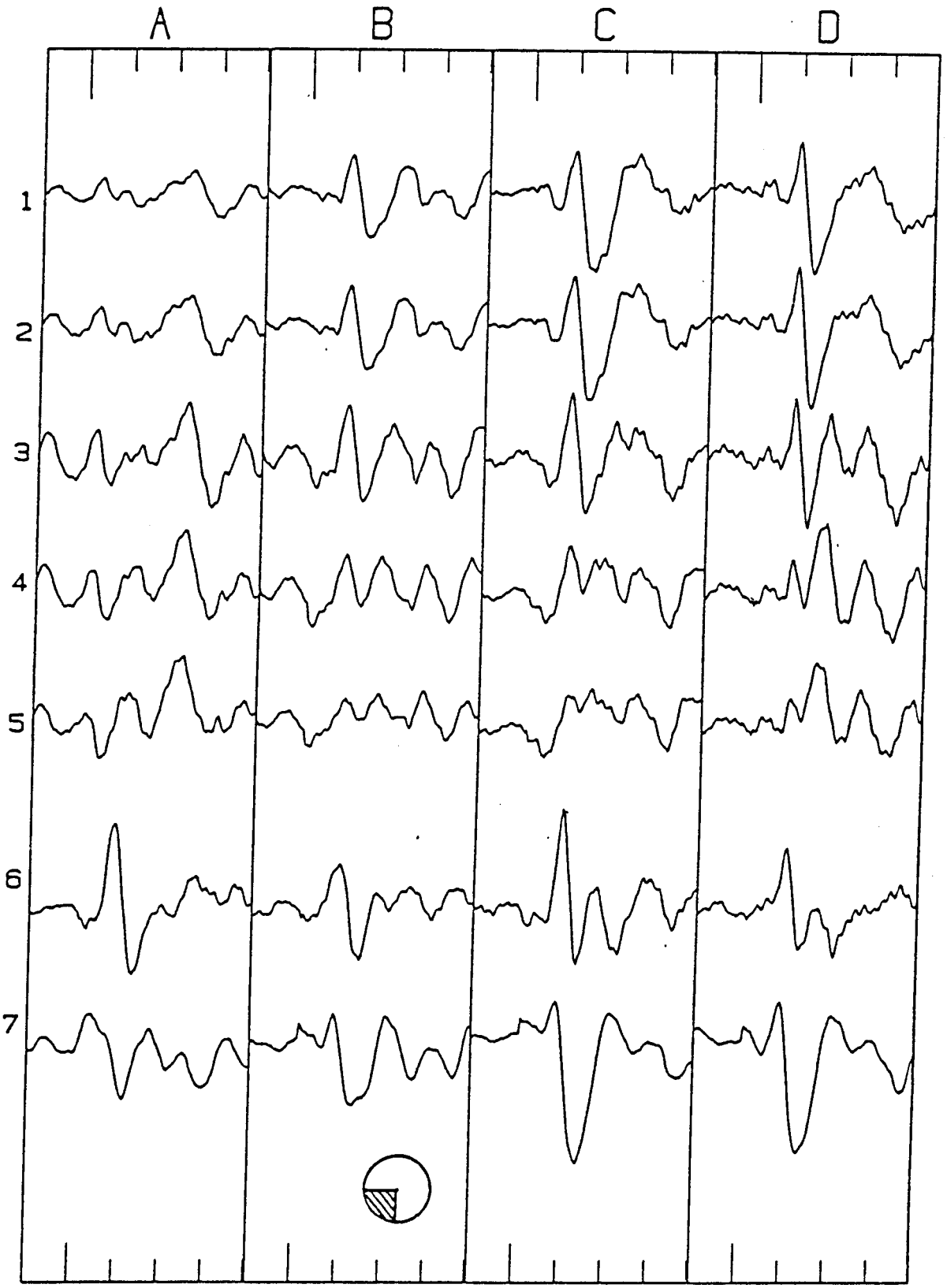


Fig. 12.2f

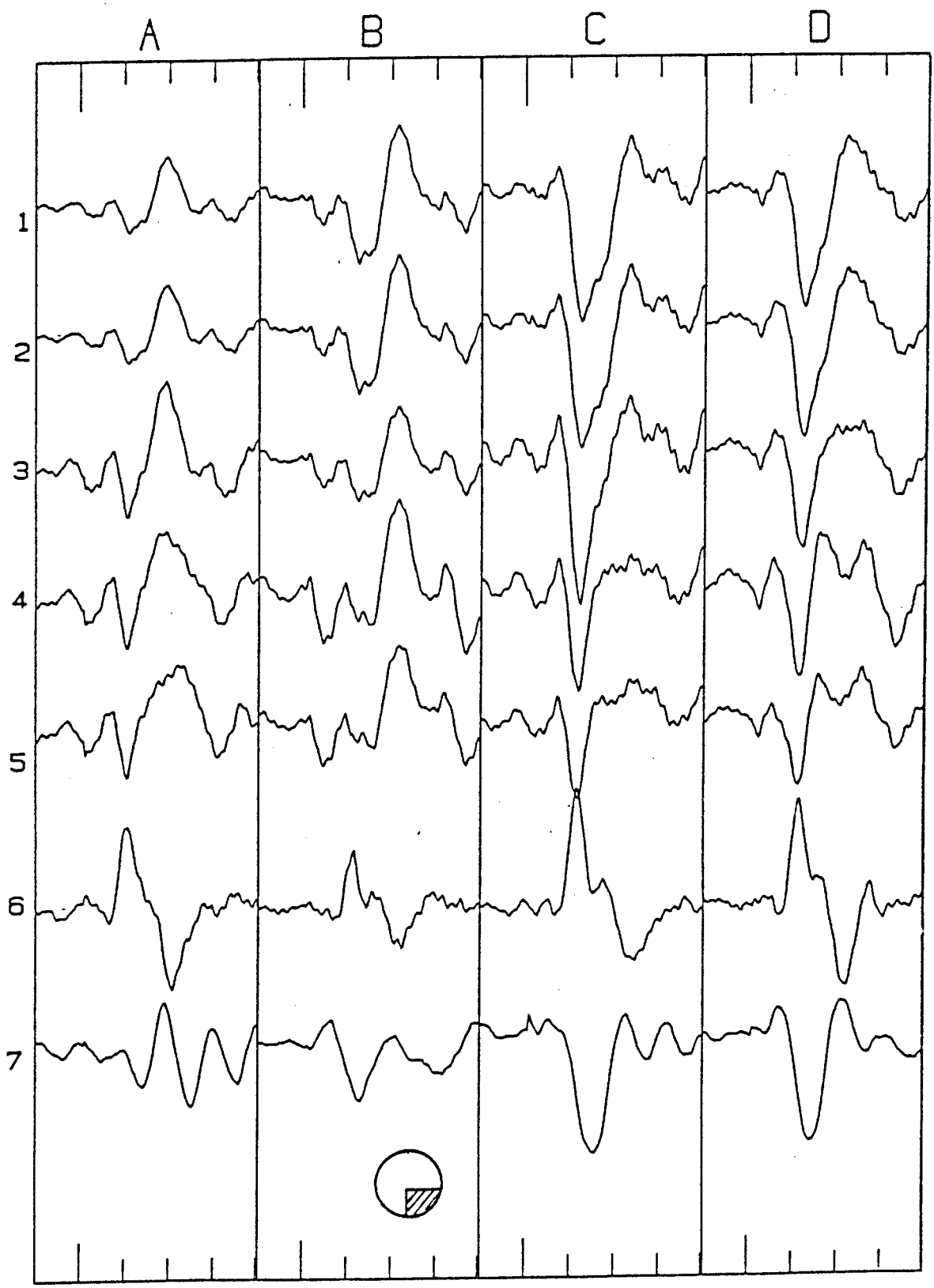


Fig. 12.2g

potential the peak latency of which again increases from condition A-C, as indeed does its amplitude. This negative peak is also evident at this electrode site with upper field stimulation.

The polarity reversal of the peak at a latency of between 109 msec (condition A) and 118 msec (condition C and D) suggest that this is the CII component. Its distribution for upper and lower field stimulation is consistent with that reported by Jeffreys and Axford (1972b) for the component of extrastriate origin, (see for example figure 1.2, chapter 1).

In figure 12.2 (c) are superimposed the waveforms recorded with left and right field stimulation. Consistent with previous data, left and right-half field stimulation elicits little activity along the midline, supporting the prediction that the generators of the upper and lower field activity lie opposite each other; their potential fields thus cancelling. Cancellation is not of course complete at each electrode site because of the asymmetrical distribution of the respective potential gradient for upper and lower half-fields. Thus, for example, with left half-field stimulation there appears to be polarity reversal above and below electrode position 3 which would be predicted from the asymmetry of the upper and lower field distribution.

At electrode position 7 there is again a negative potential greater in amplitude for colour contrast conditions than either monochromatoic or achromatic luminance contrast.

In figure 12.2 d & e, are shown the the VEPs to upper left and right quadrant stimulation. Consistent with the responses obtained to upper half-field stimulation, upper quadrant-field stimulation produces a large positive potential at electrode 1-5 and the maximum of this distribution is towards the more anterior electrodes, consistent again with the Jeffreys & Axford model for the source locus of CII. There is little difference between the distributions under the four conditions, only the latency difference reported above, are evident. With upper left quadrant stimulation the waveform at electrode 6 show a positive potential the peak of which is earlier than that of the monopolar placements, this is CI.

In figure 12.2 f & g, are shown the waveforms elicited by lower quadrant stimulation. Consistent with the upper field waveforms electrode position 7 shows a large negative potential, larger in fact,

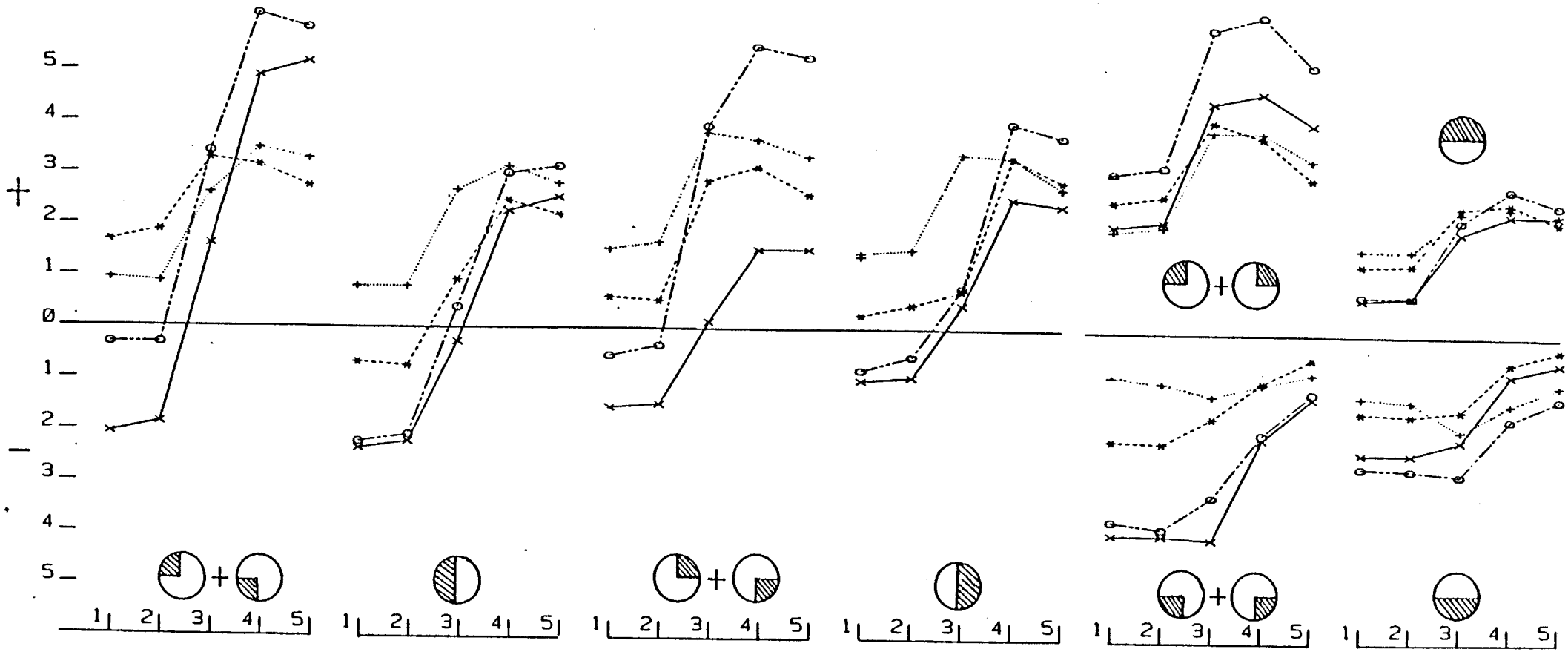

+
5
4
3
2
1
0
1
2
3
4
5
−
1 2 3 4 5

Figure 12.3

Longitudinal amplitude ditributions for the monopolarly recorded 109-120 msec sample elicited by half-field and quadrant stimulation.

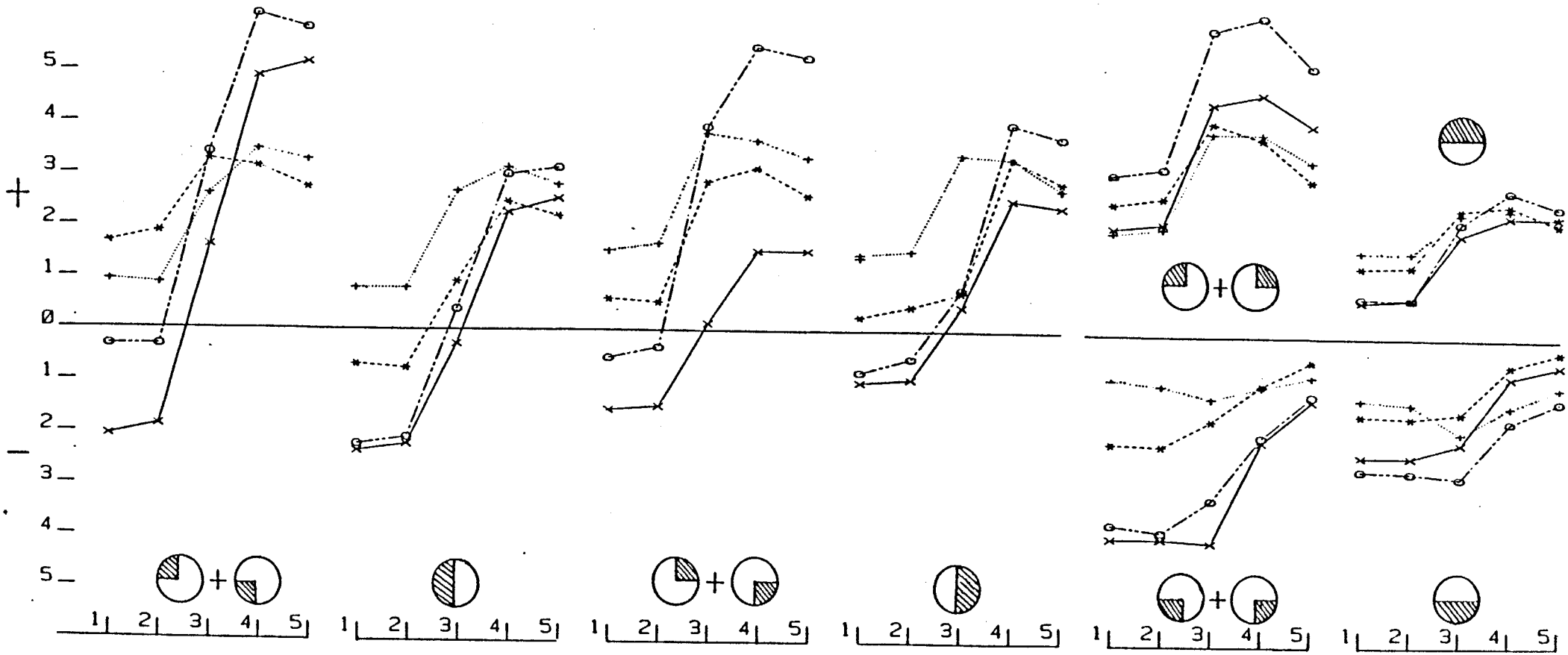
For upper and lower half-field and upper right + left quadrant and lower right + left quadrant distributions the gain has been reduced by a factor of two, for clarity of presentation. Numbers on the abcissa refer to electrode locations, see figure 12.1a.

Achromatic luminance contrast =

Monochromatic luminance contrast =

Isoluminant colour contrast =

Colour contrast + 20% luminance contrast =


+
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2
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0
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4
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1 2 3 4 5

than that obtained to upper quadrant stimulation but again maximal for colour contrast stimulation. This is the most obvious difference in these waveforms. In almost every retinal (pattern) position this peak is larger and of a longer latency than that produced by either monochromatic or achromatic patterned stimuli.

These longitudinal electrode placements reveal little CI activity consistent with the predicted striate origin of this component; it is more clearly identified with the transverse bipolar placements similar to the distribution of activity produced in this subject with larger field stimulation.

In figure 12.3 are shown the distribution of activity at a peak latency between 109 and 120 msec (peak latency will be dependent on stimulus type). Also plotted in this figure is the peak amplitude of the negative potential of similar latency recorded with lower field stimulation. Shown also are the distributions of activity, at comparable latency, produced when each of the appropriate quadrant responses are summed. For upper and lower half-field and the appropriate summed quadrant responses the gain has been reduced by a factor of 2 for convienience of representation. Despite different conditions, the resultant upper and lower field distributions are consistent with those reported by Jeffreys (1970). Upper field activity is positive going and maximal at anterior electrodes, that for lower field stimulation is negative going and maximal at posterior electrodes. The distribution of summed quadrant activity is similar to that of the appropriate half fields although there is some evidence of non-linearity.

In figures 12.4 a,b,c the half-field waveforms have been shown along with the appropriate summed quadrant responses. Despite slight differences in the form of the responses the summed waveform are similar to the half field responses which suggests that the latter are produced by independent cortical generators. It is also evident that the response to full field stimulation is the sum of opposing half-field activity, as illustrated in figure 12.4 d,e.

It would appear therefore that there is little difference between the VEPs evoked by the four types of stimulus used in this experiment. For the main pattern specific component, CII, the major difference between the four conditions is the increase in peak latency, consistent with the results of chapter 11.

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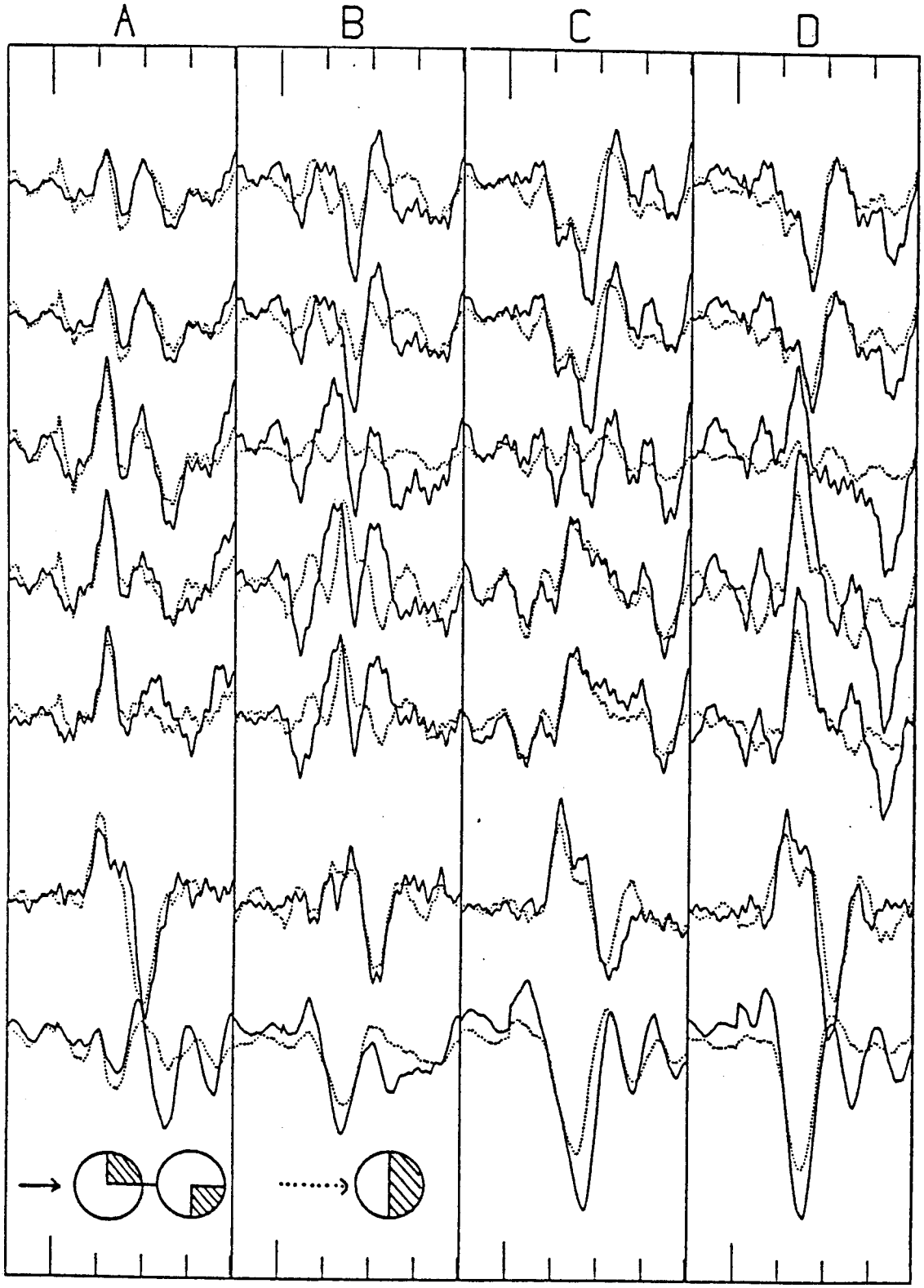

Fig. 12.4a

Figure 12.4a-e

Half field VEPs superimposed on the summed waveforms recorded from two individualy stimulated quadrants. See text for discussion.

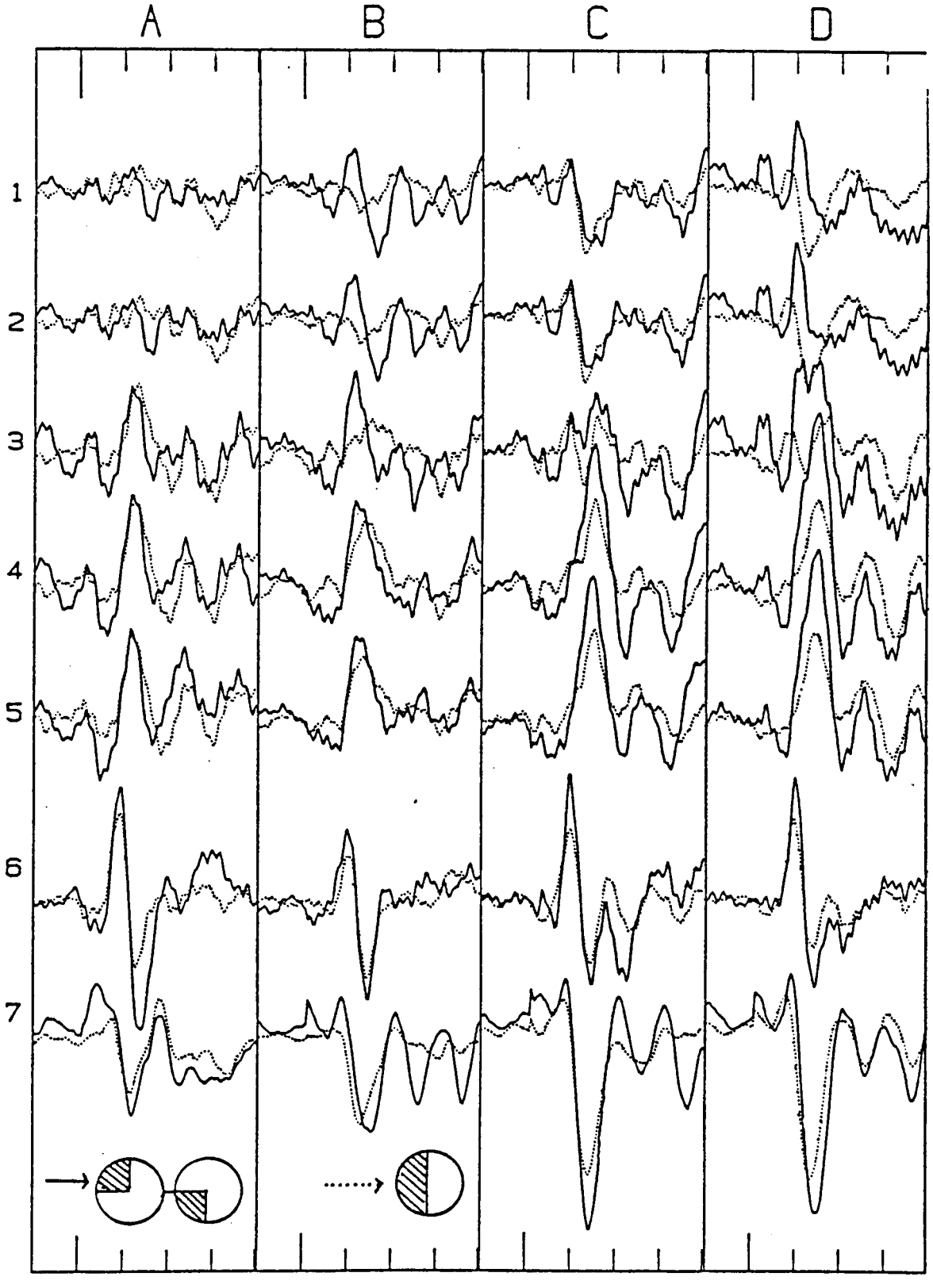

Fig. 12.4b

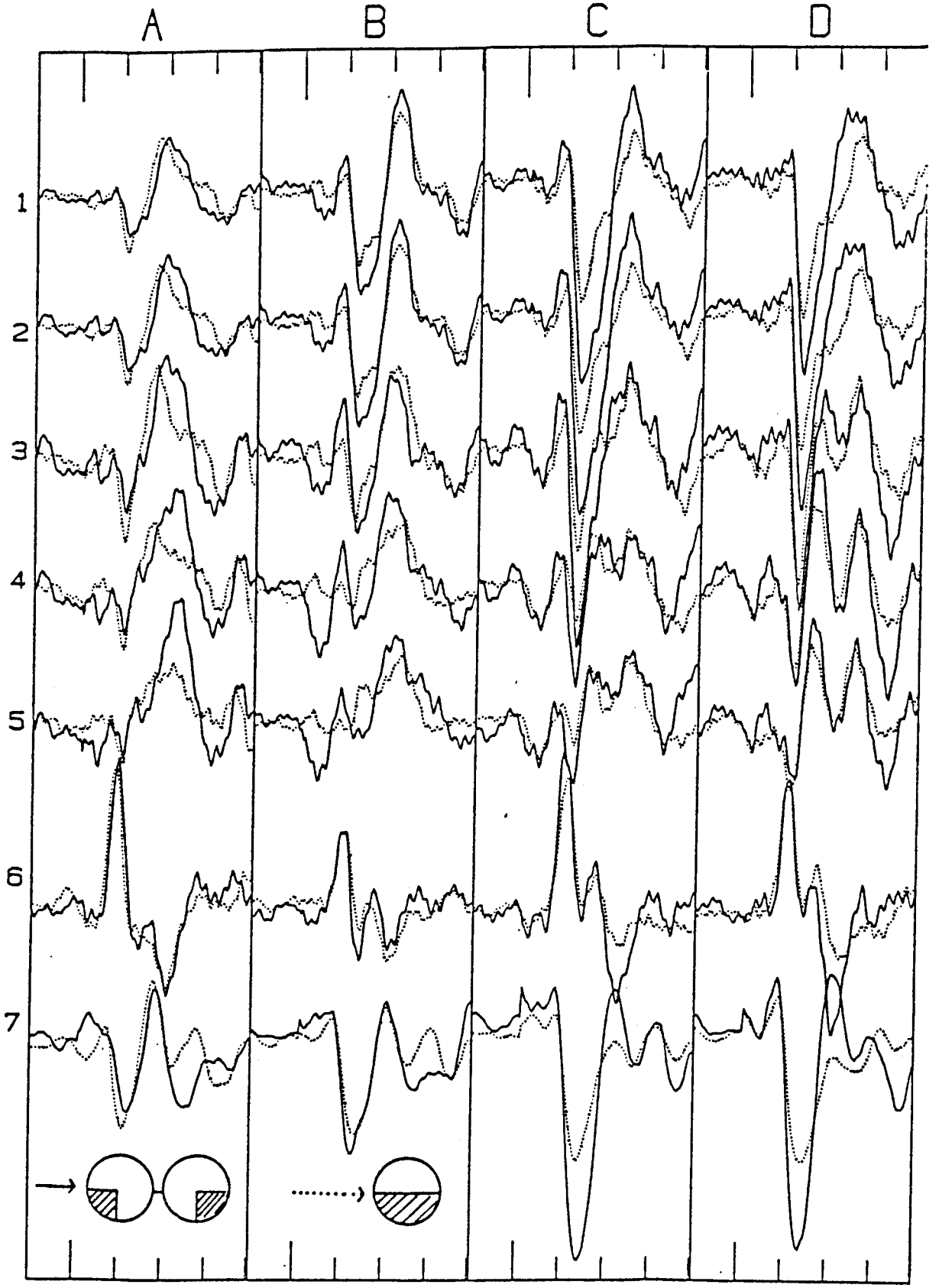

Fig. 12.4c

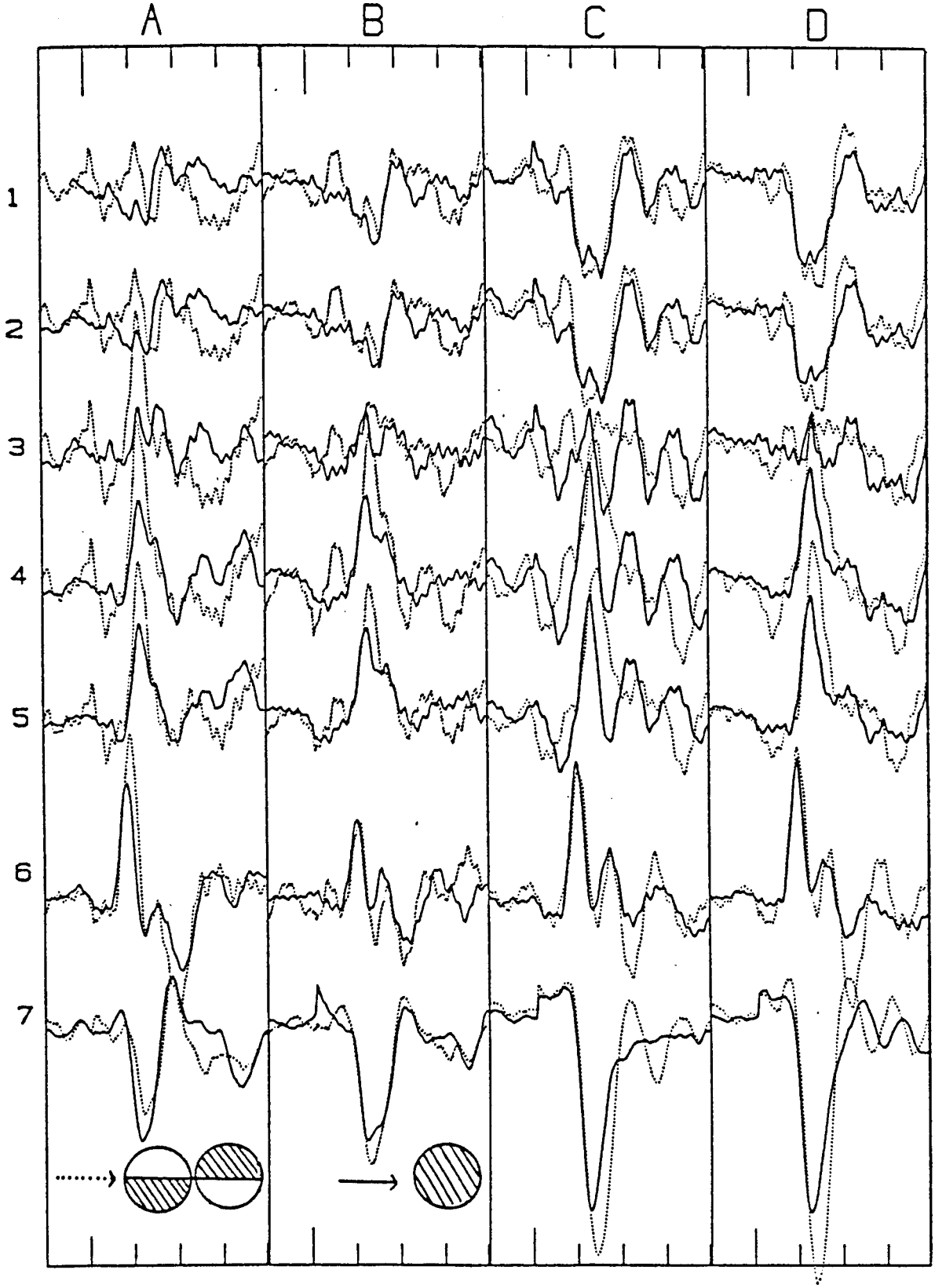

Fig. 12.4d

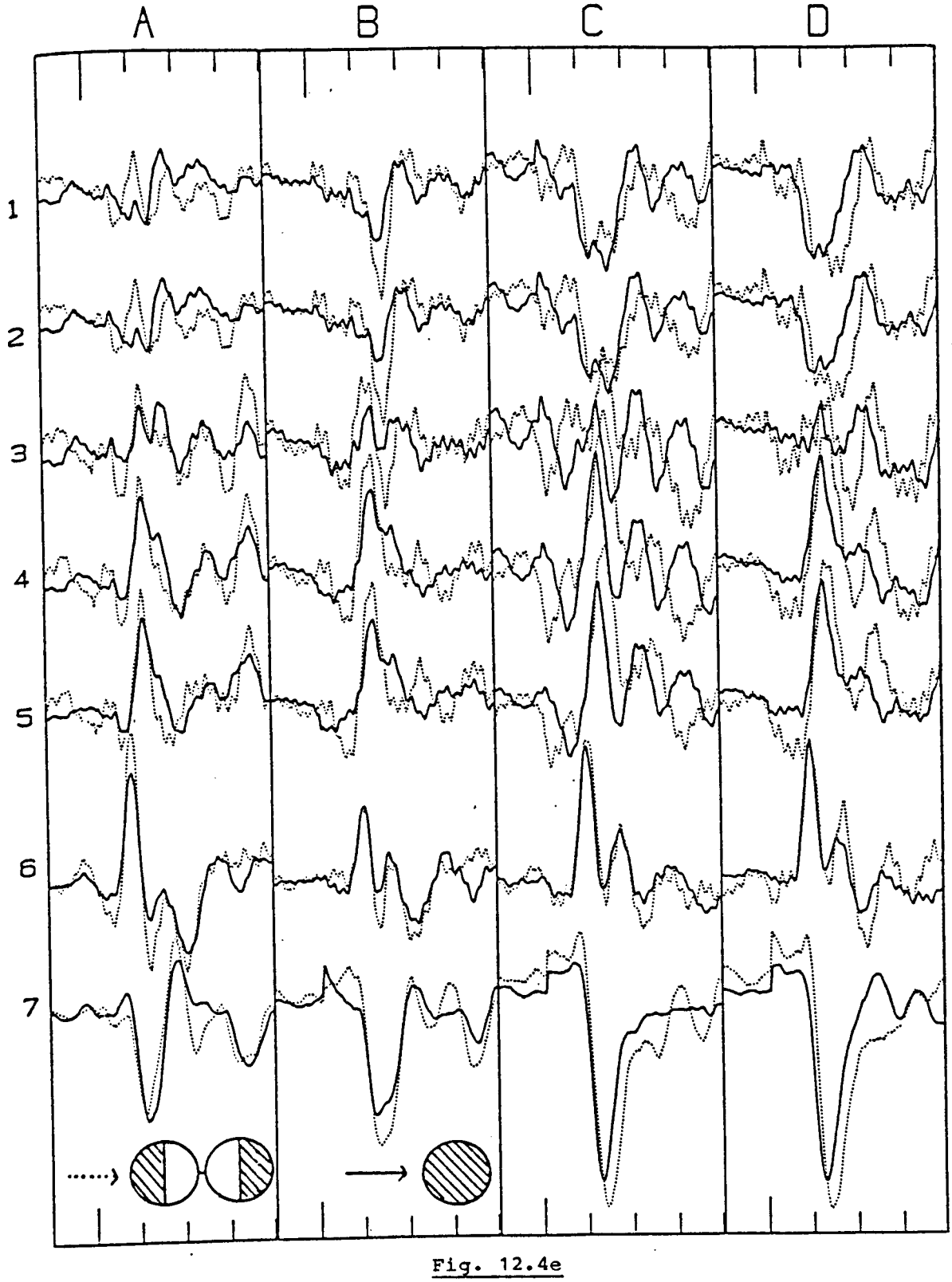

Fig. 12.4e

12.2:- Longitudinal mapping subject II

The previous experiment, whilst not providing conclusive evidence of any new VEP component specific to colour contrast stimulation, did suggest that at the placement 7 (recorded between electrodes 1-5 (see figure 12.1) a large negative potential, evident to all types of stimulus, is particularly pronounced with colour contrast stimulation. A possible explanation for this result is that the colour contrast patterns stimulate a further population of cortical neurons, selective for wavelength differences. Since there is no evidence of a distinct peak in the monopolarly recorded waveforms it is possible that another cortical generator contributes to the activity, in addition to those responding to both luminance and colour contrast stimuli. This explanation would not only account for the increase in amplitude of the response but also the lengthening of its time course, as it is possible that the two areas are not in distinct anatomical regions, but in functionally distinct ones which lie in close proximity as indeed do the visual areas within area 18 of the rhesus monkey.

In the following experiment, a longitudinal mapping was undertaken for a further subject, whose distribution of pattern-onset components was well known, in an attempt to determine the generality of the above results.

Procedure

The general procedure was similar to that reported above, although in this case only three conditions were used:-

A:- achromatic luminance contrast.

B:- monochromatic luminance contrast.

C:- isoluminant colour contrast.

The electrode positions and reference numbers are given in figure 12.1a.

Results

In figure 12.5a-g are shown the distributions of activity produced by stimulating all half-fields and quadrants under the three conditions used. As with the previous subject, upper and lower half-field stimulation produces, respectively, a large positive and a negative potential at the longitudinal monopolar electrodes, with a latency of

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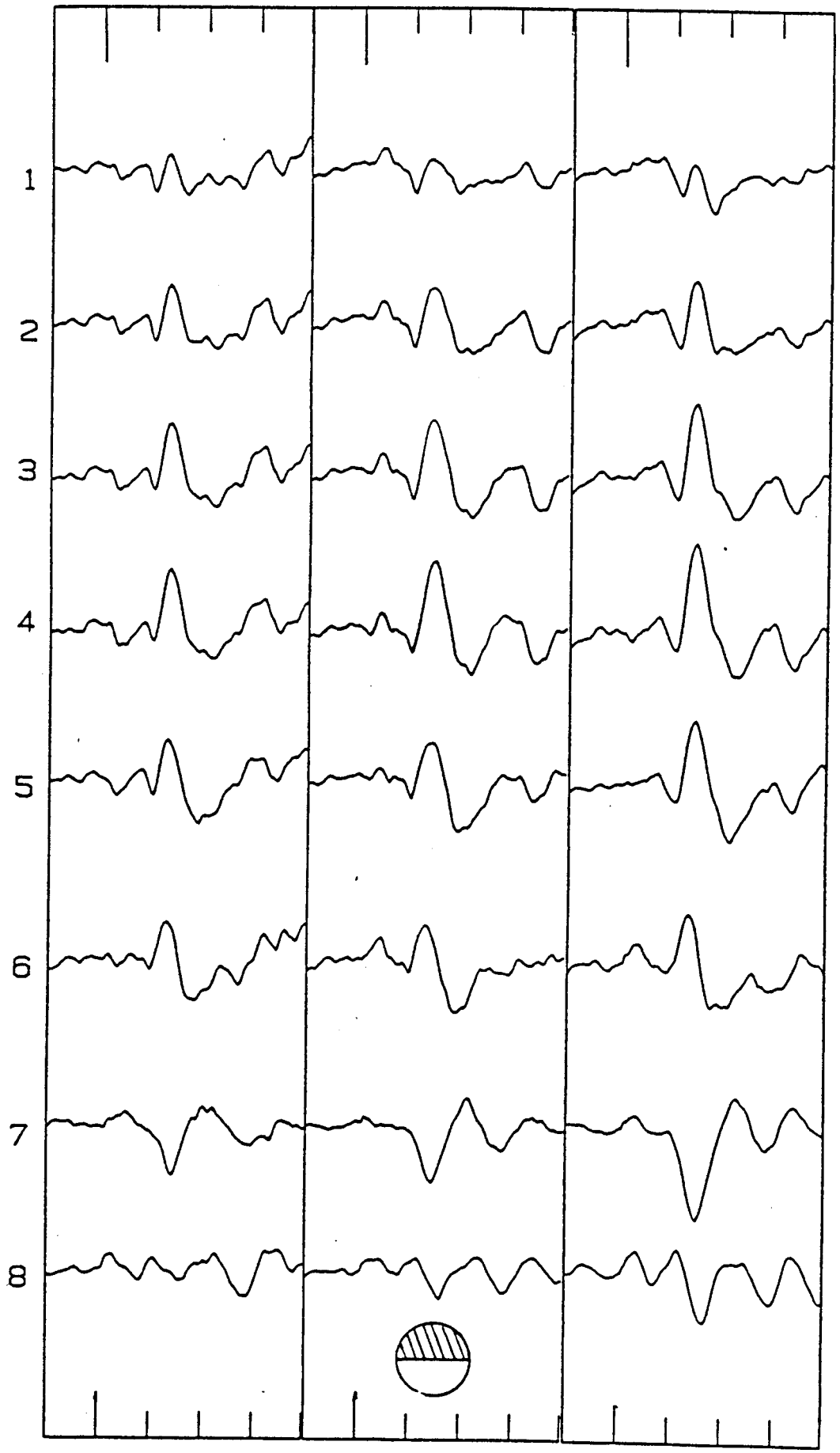


Fig. 12.5a

Figure 12.5a-g

Half-field and quadrant VEPs for subject D.A.J. under achromatic luminance contrast (column 1) monochromatic luminance contrast (column 2) and isoluminant colour contrast (column 3). Numbers refer to electrode locations shown in figure 12.1.B.

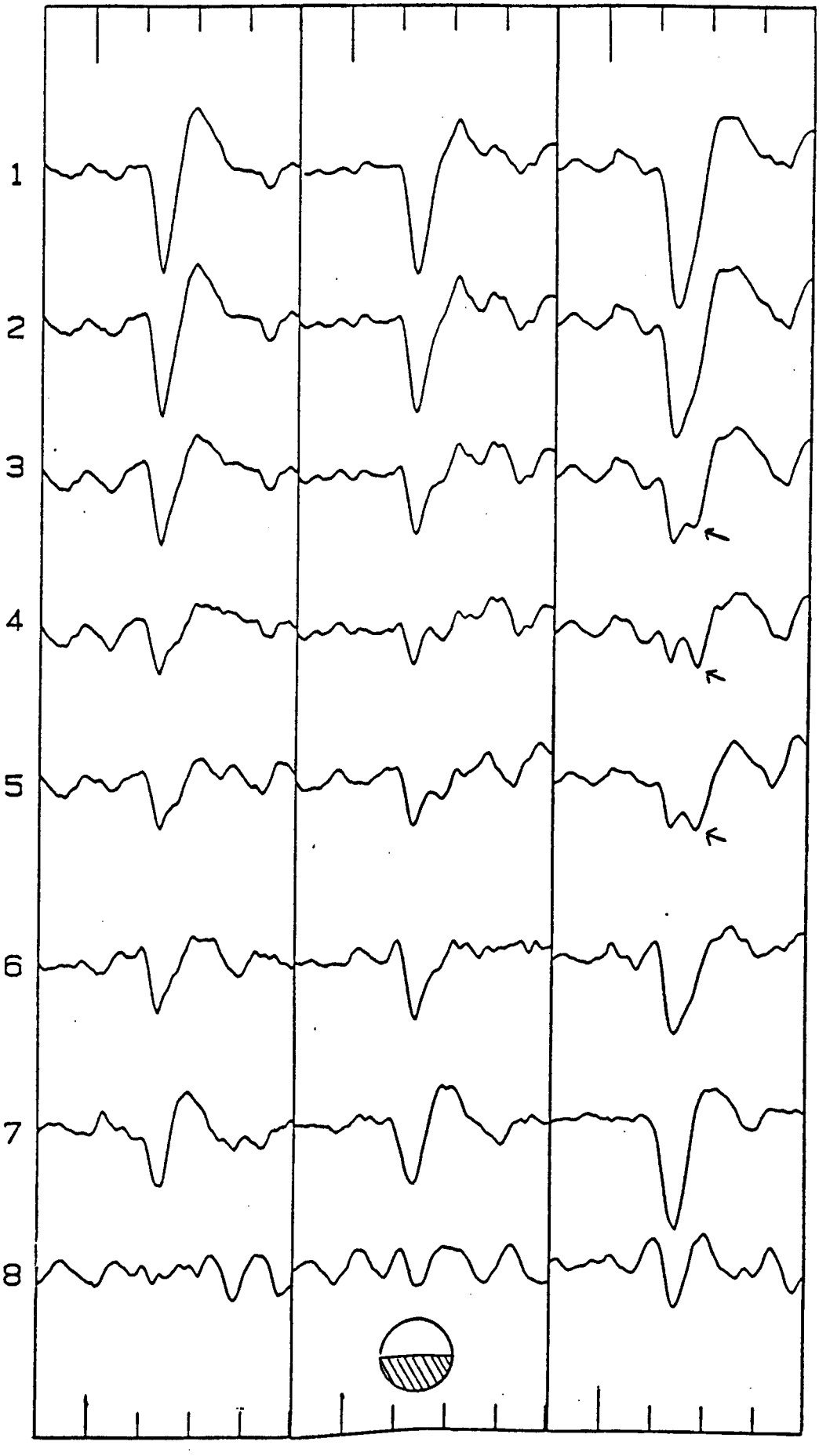


Fig. 12.5b

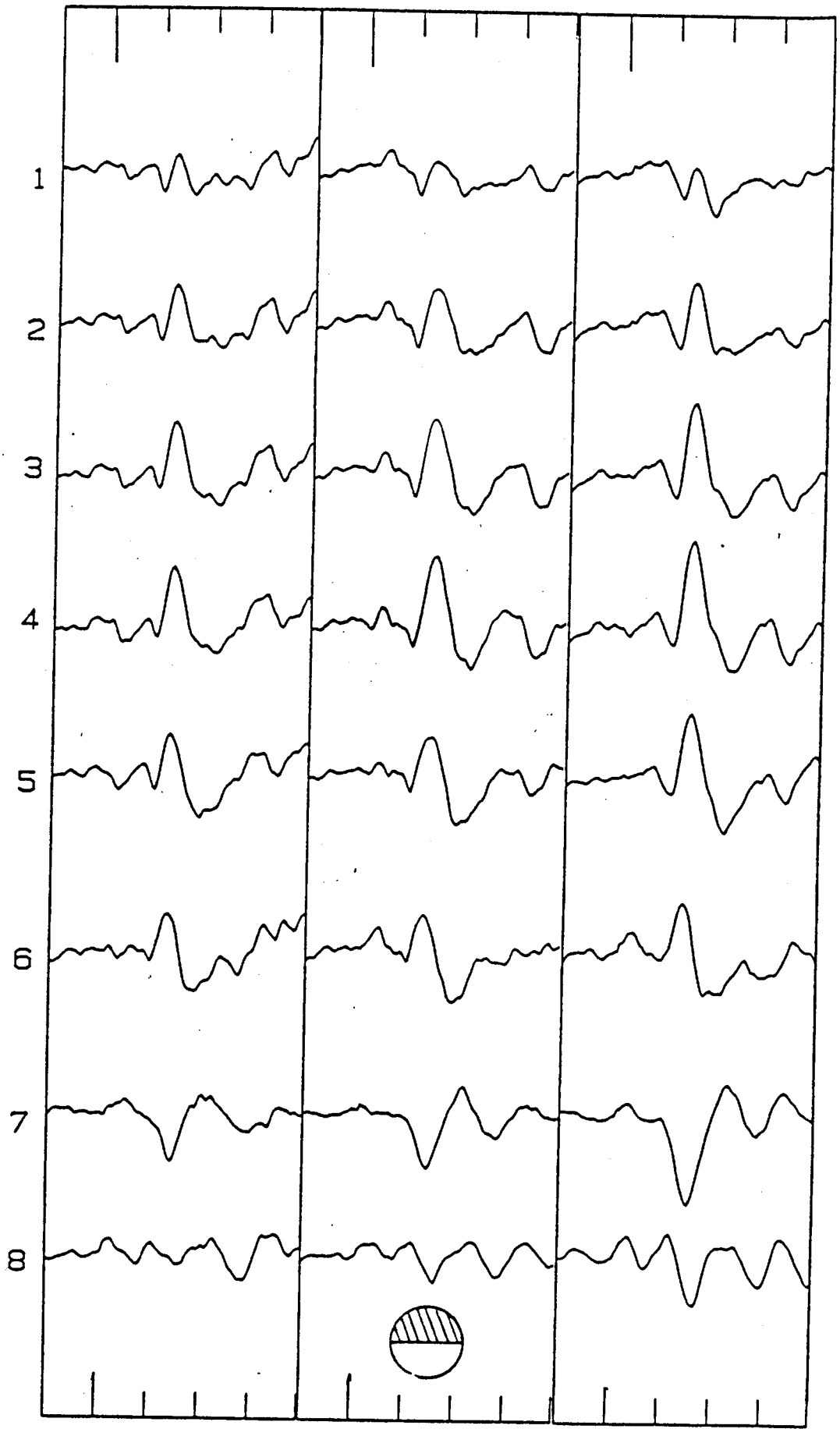


Fig. 12.5a

Figure 12.5a-g

Half-field and quadrant VEPs for subject D.A.J. under achromatic luminance contrast (column 1) monochromatic luminance contrast (column 2) and isoluminant colour contrast (column 3). Numbers refer to electrode locations shown in figure 12.1.B.

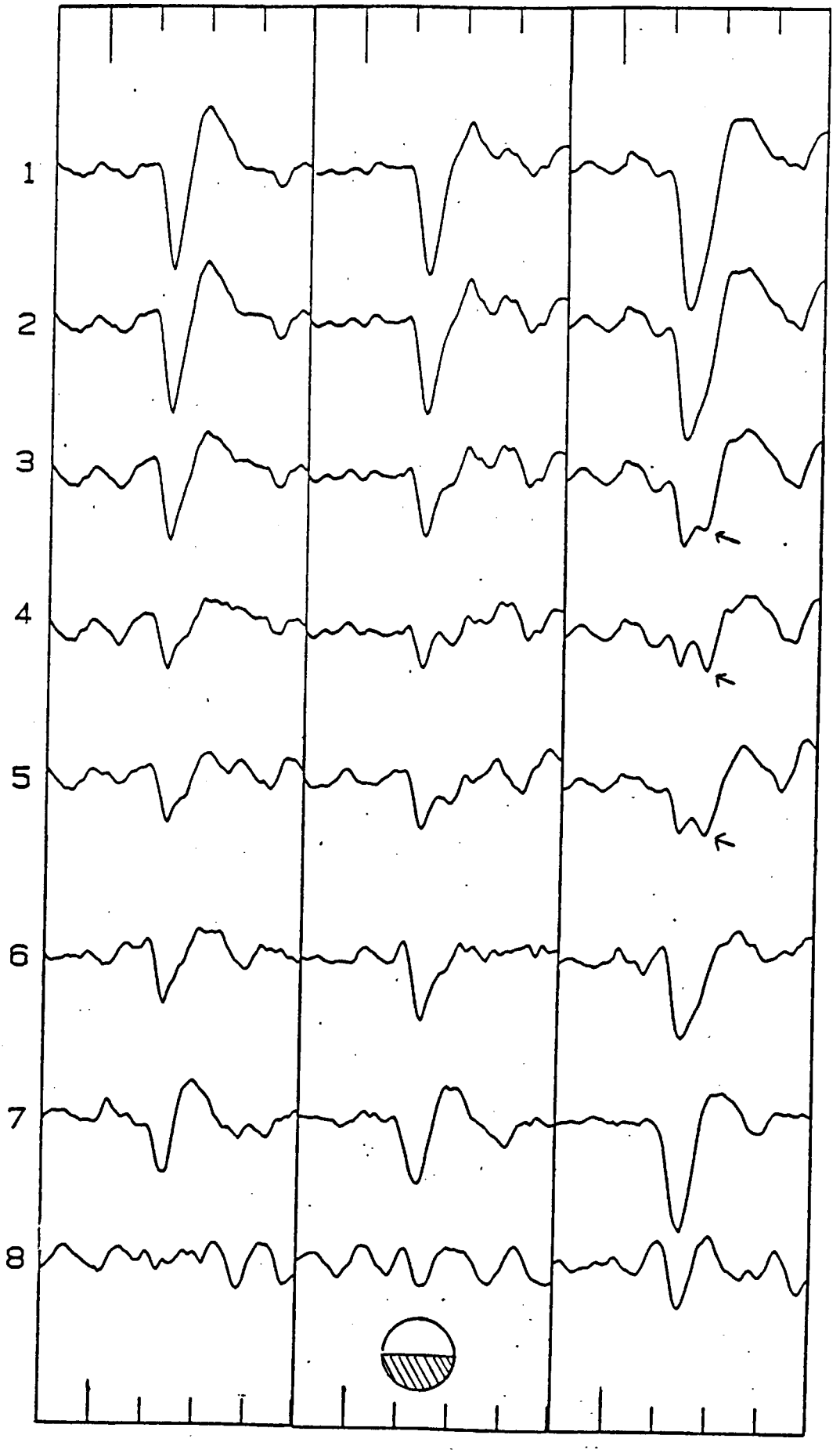


Fig. 12.5b

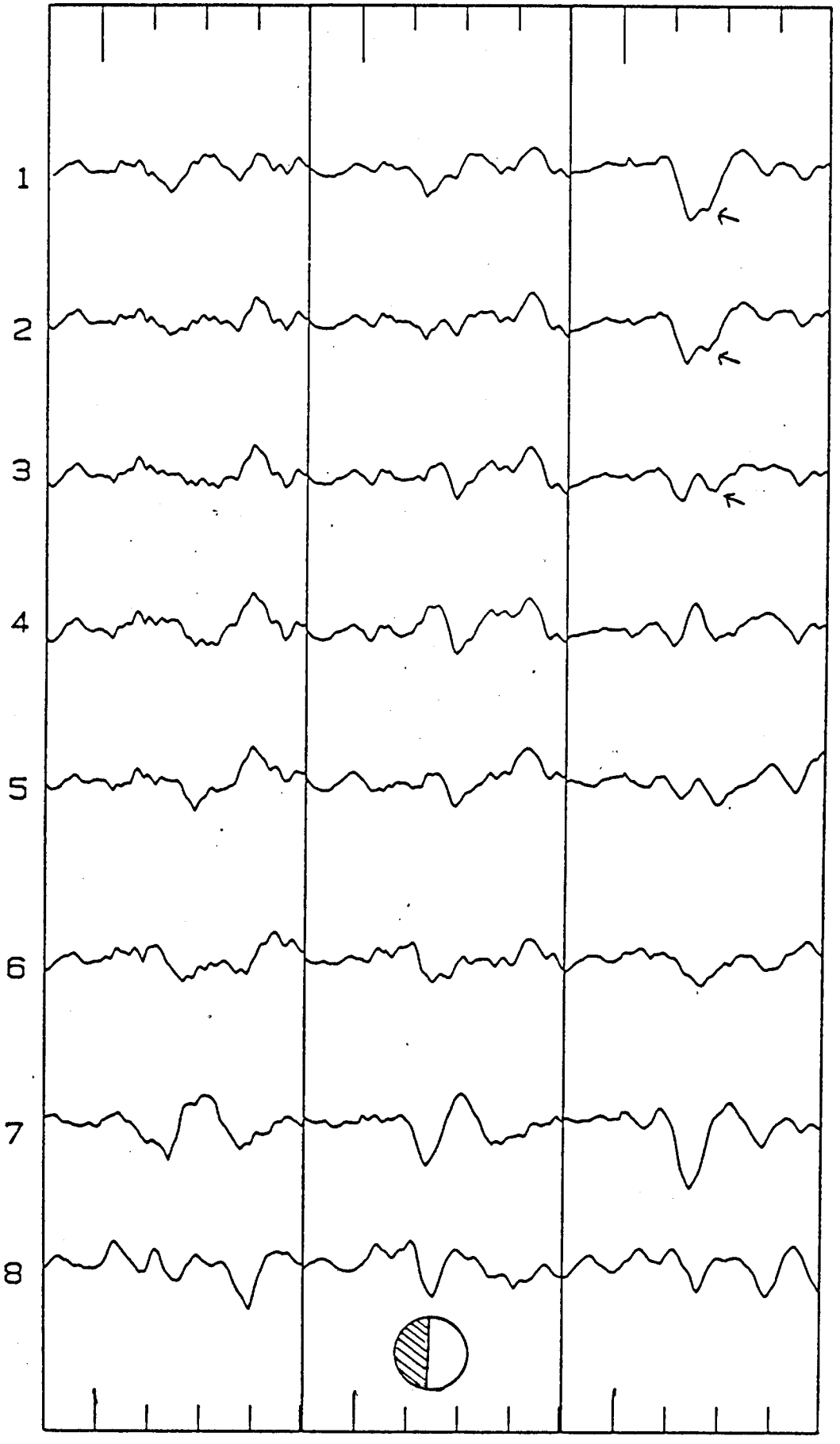


Fig. 12.5c

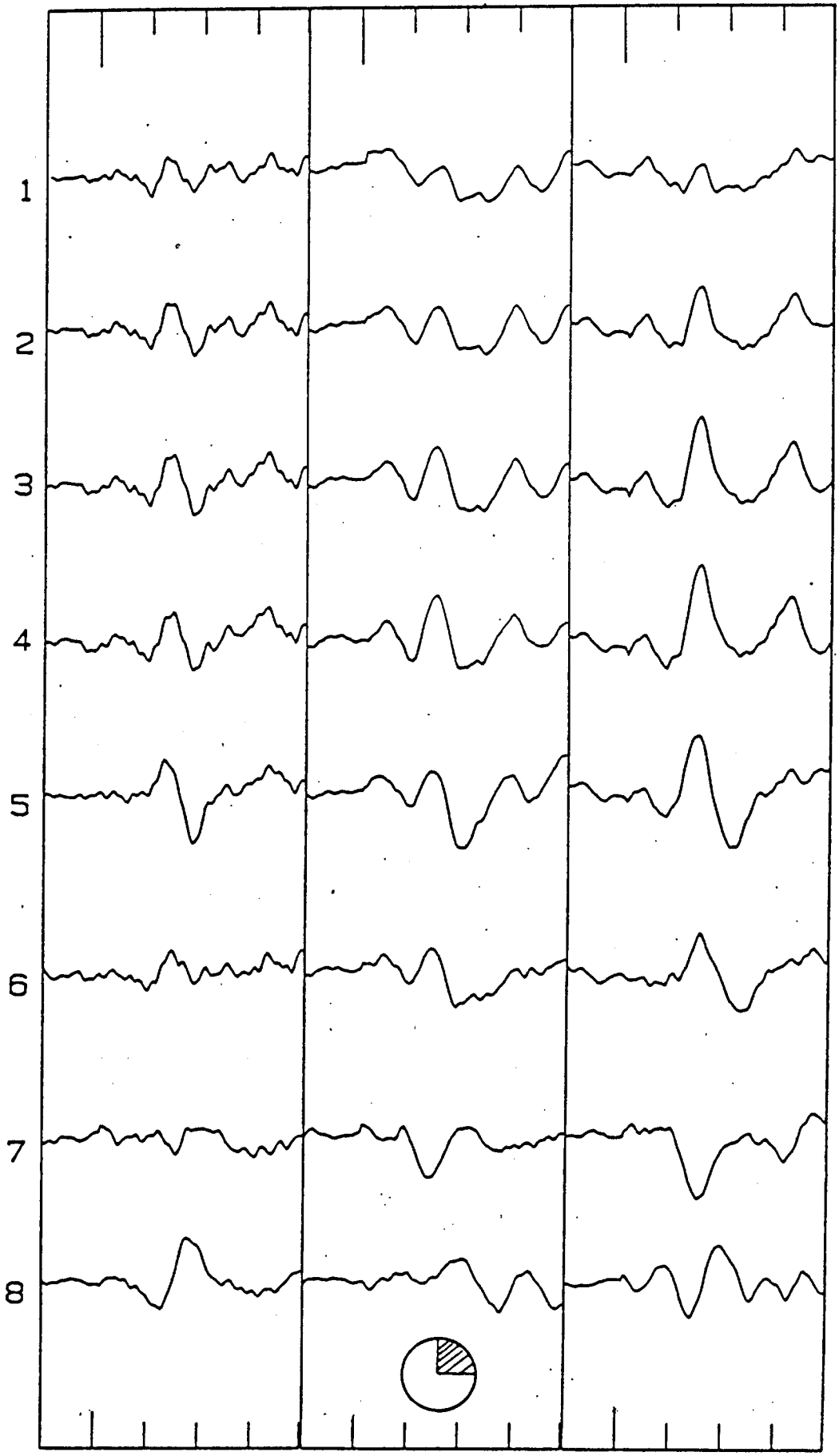


Fig. 12.5d

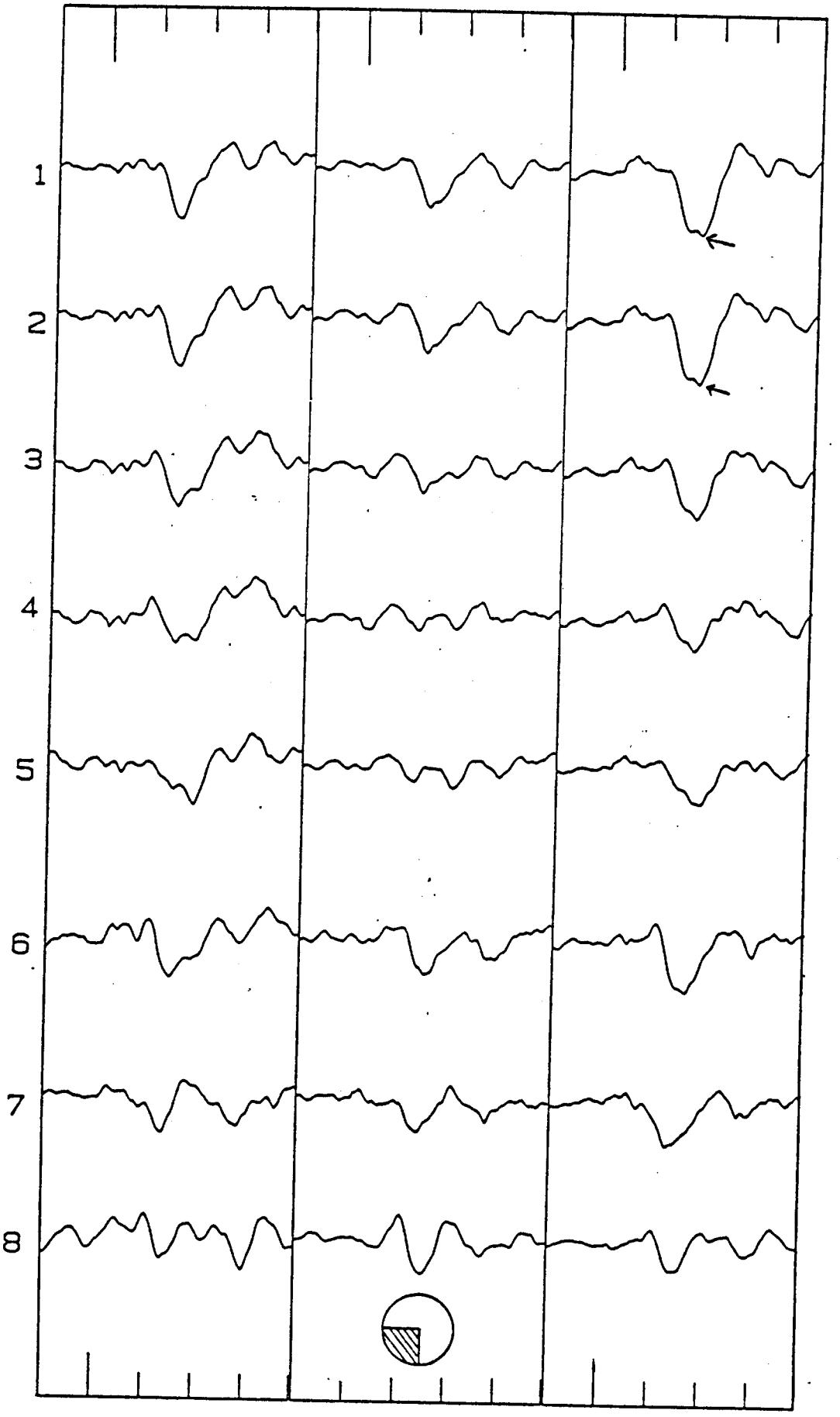


Fig. 12.5e

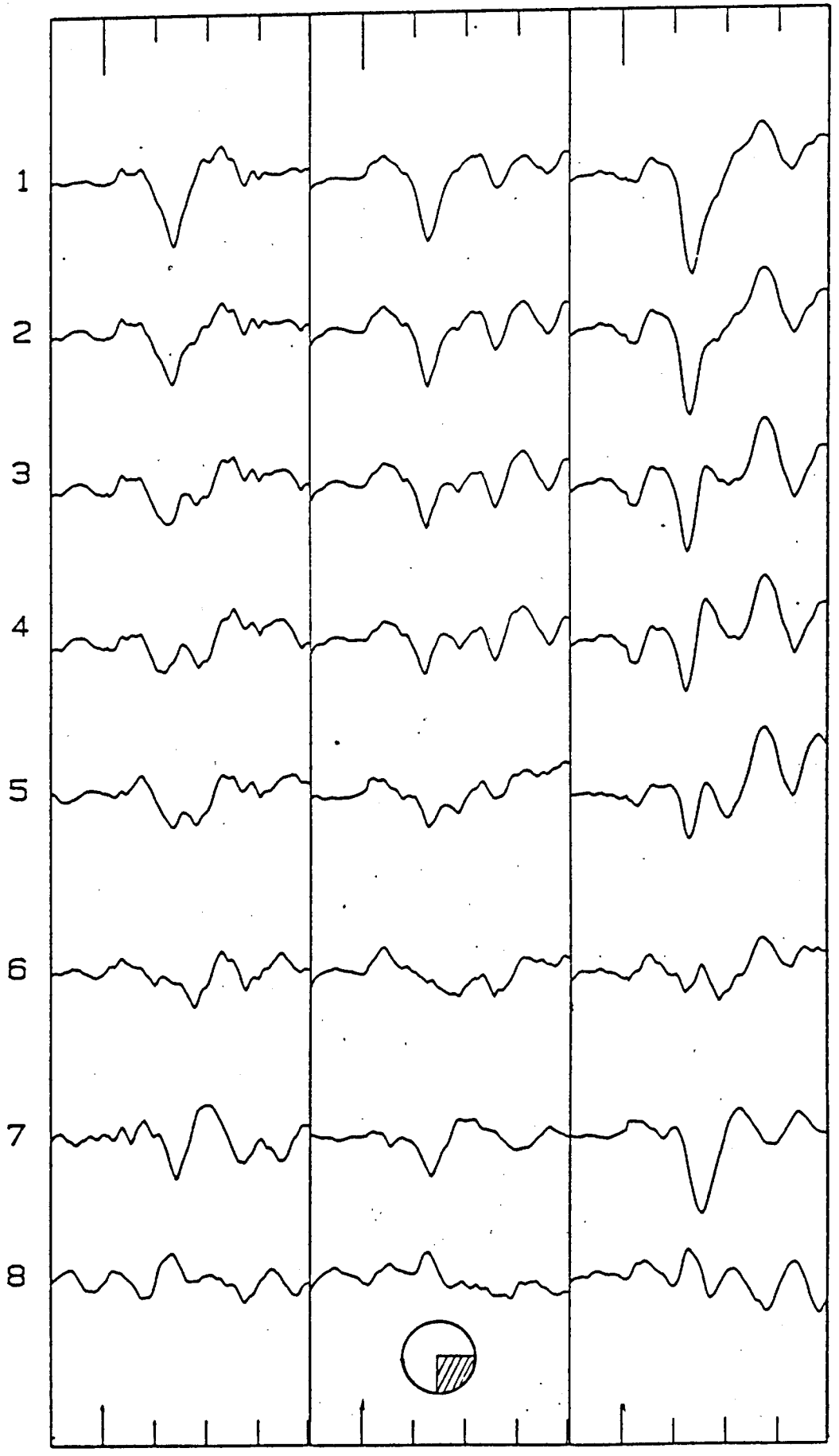


Fig. 12.5f

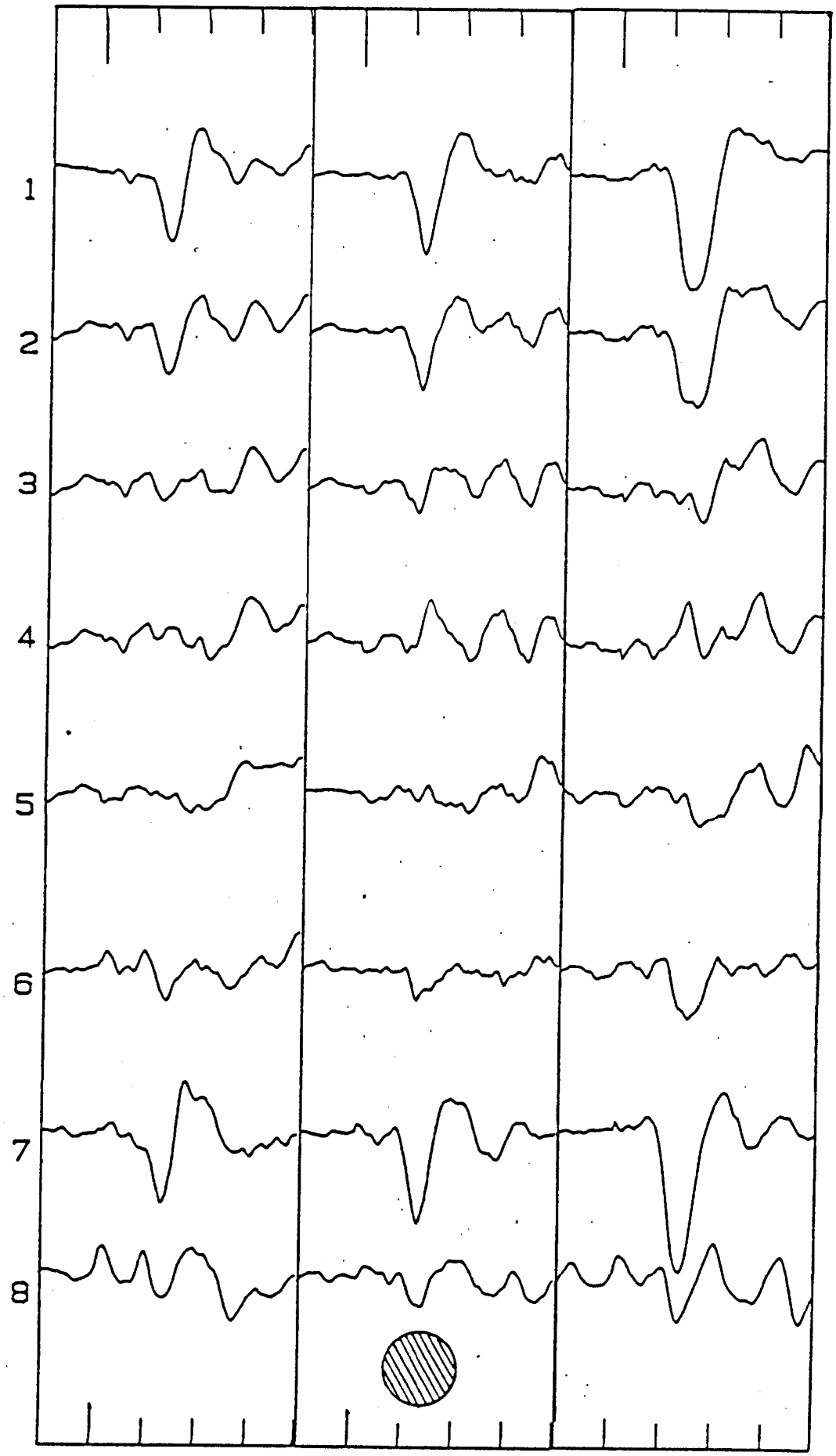


Fig. 12.5g

between 109-124 msec. Again, peak latency increases from condition A to C, although the amplitude of the VEP is generally larger for the latter.

In this subject there is little evidence of a CI component to right half-field stimulation, despite the fact that this position is optimal for recording the component, as was shown in chapter 3, 4 and 5. The absence of CI can be explained by the limited field size and by the fact that this component is small for this subject, even with larger fields of stimulation, (see chapter 9).

Thus these waveforms are dominated by CII, which, consistent with the model of Jeffreys & Axford (1972b), is maximal in amplitude at the anterior electrodes with upper field stimulation and at the posterior electrodes for lower half and lower quadrant stimulation. Because lower and upper quadrants produce activity of opposite polarity, the response to left and right field stimulation should produce cancellation at all electrode sites. However because of the asymmetrical distribution of CII for upper and lower fields, cancellation is not complete, particularly at posterior electrodes; a feature similar to that observed for subject MJM.

The picture is further complicated by the occurrence of a secondary negative peak particularly pronounced with lower half-field and lower left quadrant field stimulation, and arrowed for clarity in figures 12.5b,c & e. This peak appears to have a more anterior distribution than that of CII. However this may reflect the fact that at the posterior electrode, CII is of maximal amplitude and thus will tend to 'mask' this secondary peak. The secondary negative peak is also evident at electrode placement 5, which suggest that it may also appear in a transverse mapping.

As with subject MJM, bipolar recording between electrodes 1-4 produces a negative potential which is larger and of a longer latency and time course for colour contrast as compared to either monochromatic or achromatic luminance contrast (see for example the full field VEPs shown in figure 12.5g). However, unlike the previous subject, this peak is similar to that recorded at the monopolar placements in showing little evidence of non-linear quadrant field summation, as is shown in figures 12.6a-b where VEPs recorded to upper and lower field stimulation have been plotted along with waveforms obtained by summing responses fromm the appropriate quadrants. The fact that colour

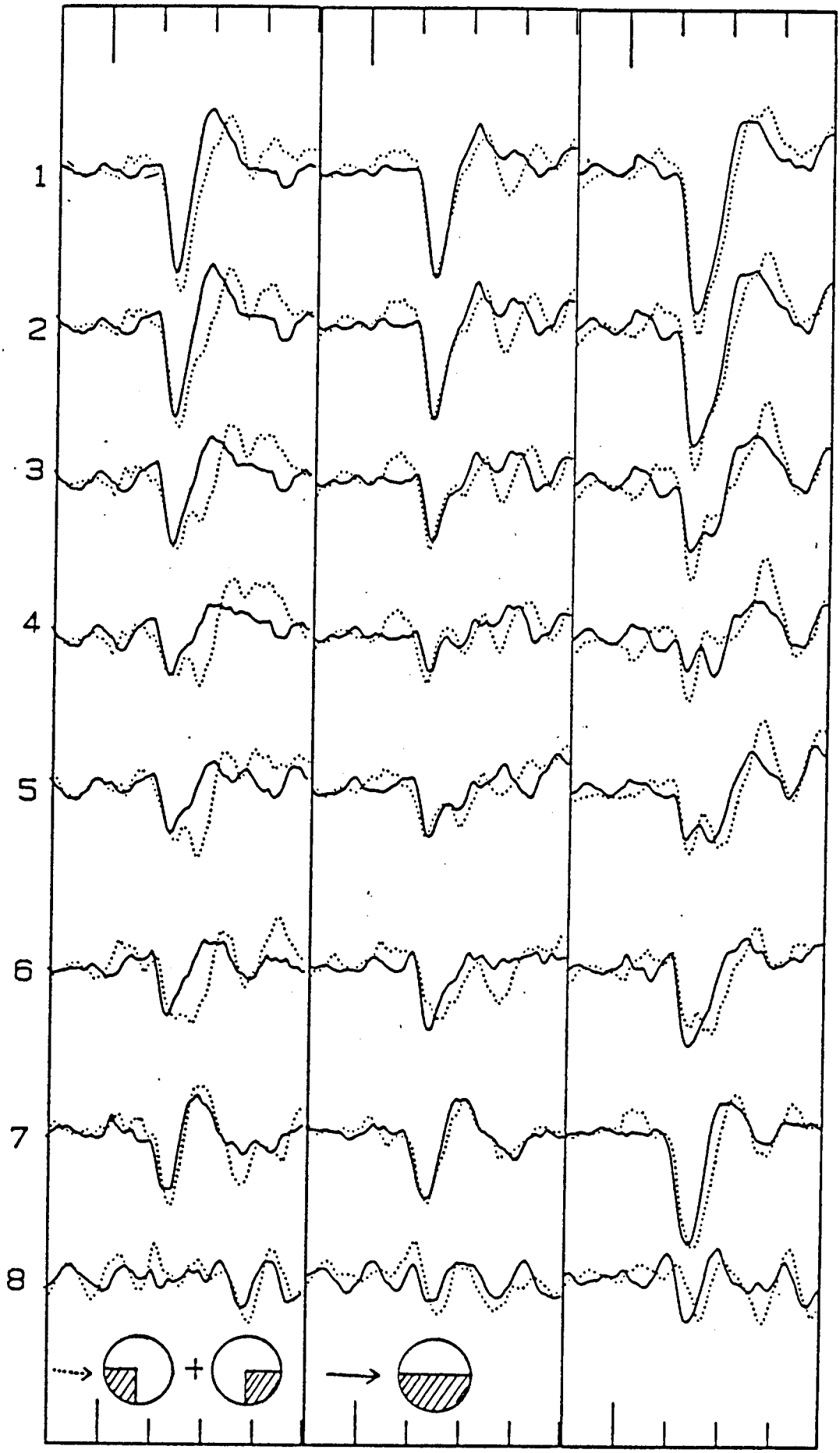


Fig. 12.6b

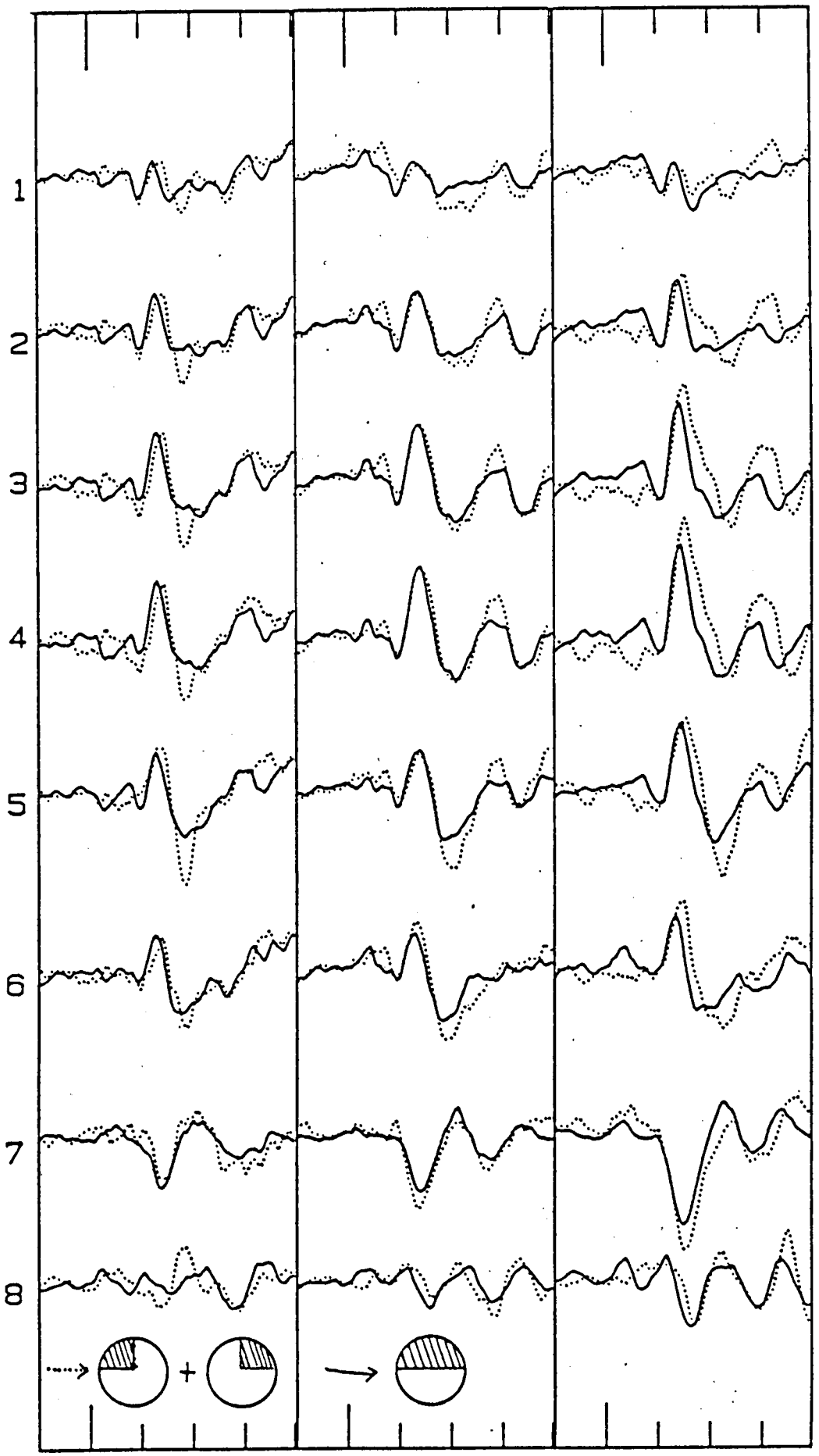


Fig. 12.6a

Figure 12.6a-b.
Superimposed half-field and summed quadrant VEPs for subject D.J.A.

contrast stimulation produces a peak of longer latency and time course suggests that these stimuli activate some population of neurons particularly sensitive to wavelength differences.

Further longitudinal mappings will be needed to determine the exact nature of this activity.

12.3:- Transverse distribution:- Subject I. Procedure

In the following study the distribution of activity was recorded from a transverse row of electrodes situated 4 cm above the inion each electrode being 2.5 cm apart as shown in figure 12.1 . Thus electrode 3 is situated on the midline electrode 2, 2.5 cm to the left and electrode 1, 2.5 cm to the left of that. Position 6 is once again the standard position for recording CI, that is bipolarly between electrode 1 and 5. Electrode 7 is a bipolar placement recorded between electrodes 2.5 cm each side of the midline and 2.5 cm above the inion.

The procedure was to record responses to isoluminant colour contrast, maximal monochromatic luminance contrast (black squares on red surround) and achromatic luminance contrast patterns presented separately in each half field and quadrant. VEPs were also recorded to isoluminant colour contrast, with a neutral density filter of 80 % transmission inserted in the green field, illuminating the pattern elements. For achromatic stimulation the coloured filter were removed from one of the fields which was then matched by flicker photometery with the one of the two remaining fields. This done, the coloured filter was then removed from this field and it in turn matched with the achromatic field. The remaining coloured field was then matched in luminance with the previous field. In these experiments 7 runs of 10 sweeps were undertaken for each condition. Stimulus duration was 30 msec.

Results and Discussion

CI:- With the small field size used in this study the CI component is not readily identified. It can however be recorded when the left half-field or the lower left quadrant are stimulated, as shown in figure 12.7a & b.. The resultant peak has a latency of 90-105 msec, increasing from condition A-C, and is maximal at the contralateral electrodes

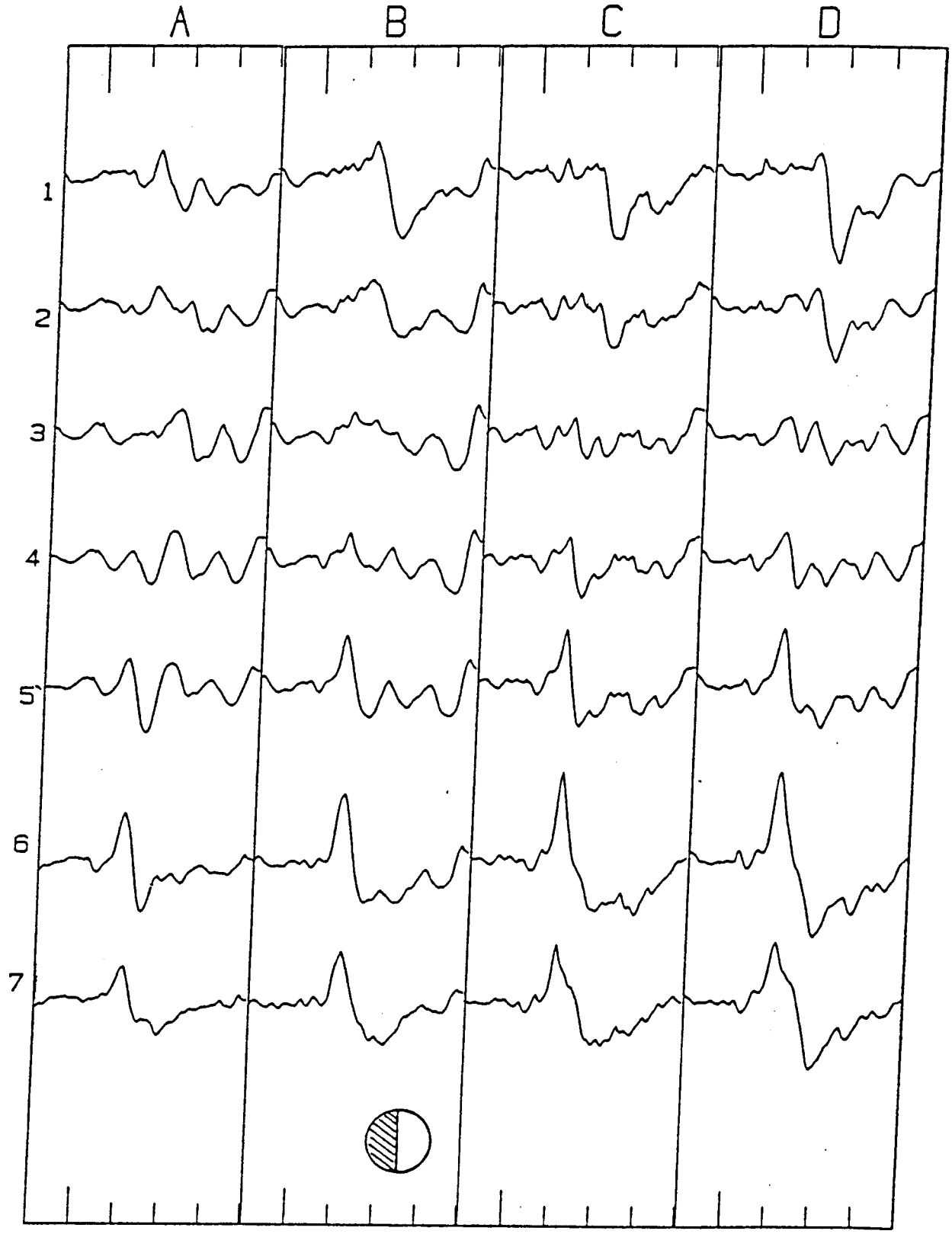


Fig. 12.7a

Figure 12.7a-j

Waveforms recorded from a tranverse row of electrodes for subject M.J.M. Electrode locations 6 & 7 are bipolar, see figure 12.1.

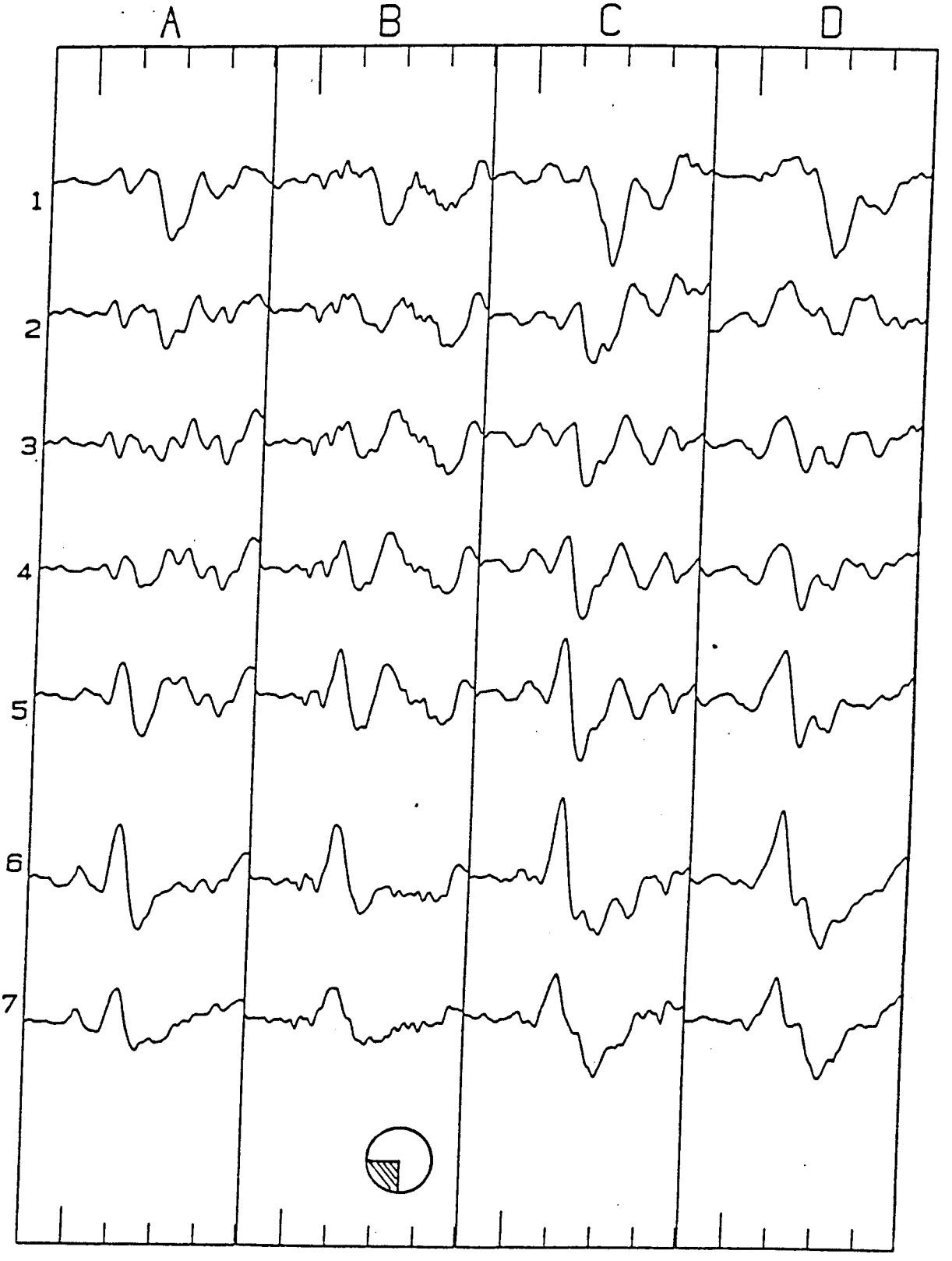


Fig. 12.7b

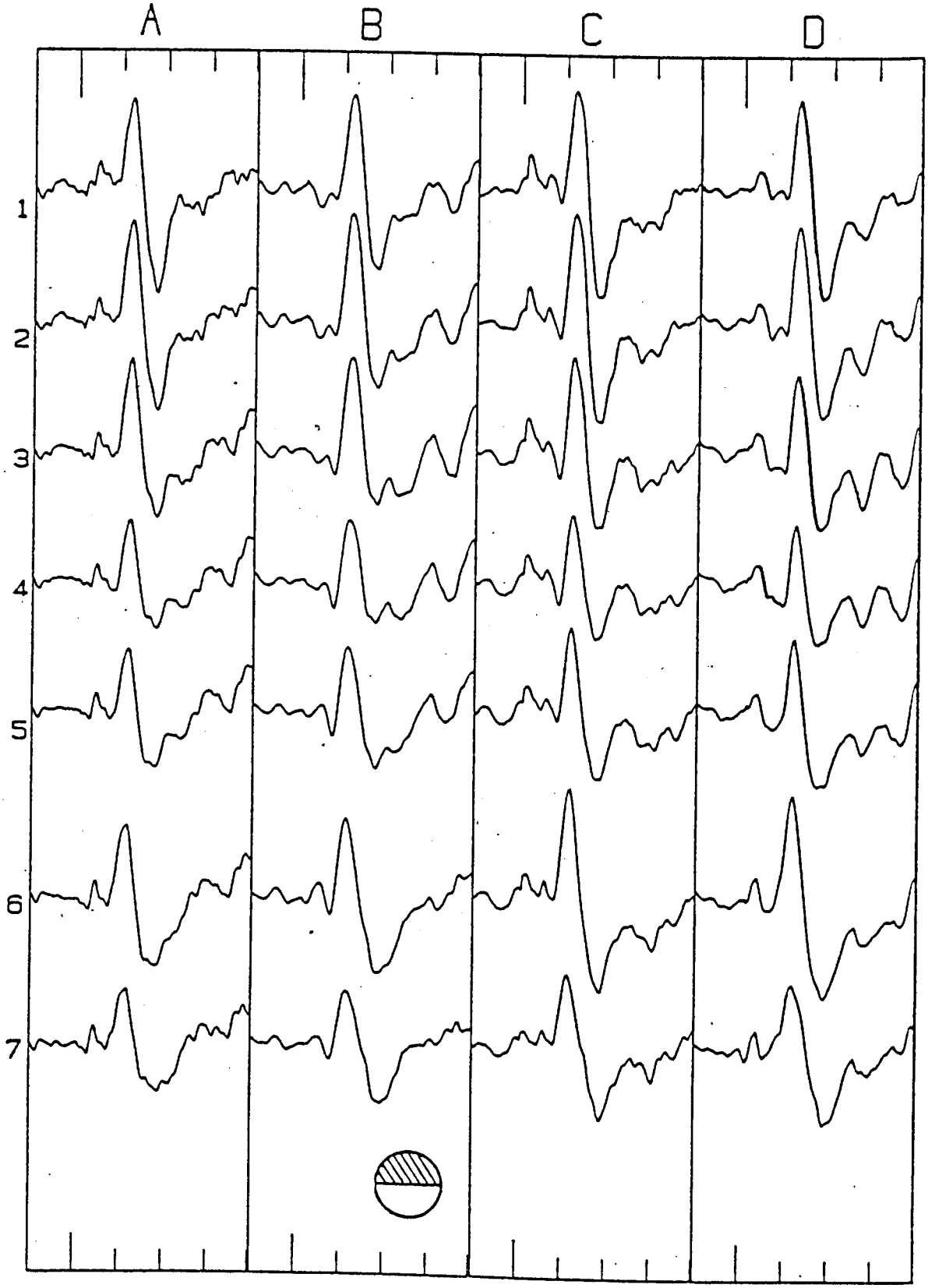


Fig. 12.7c

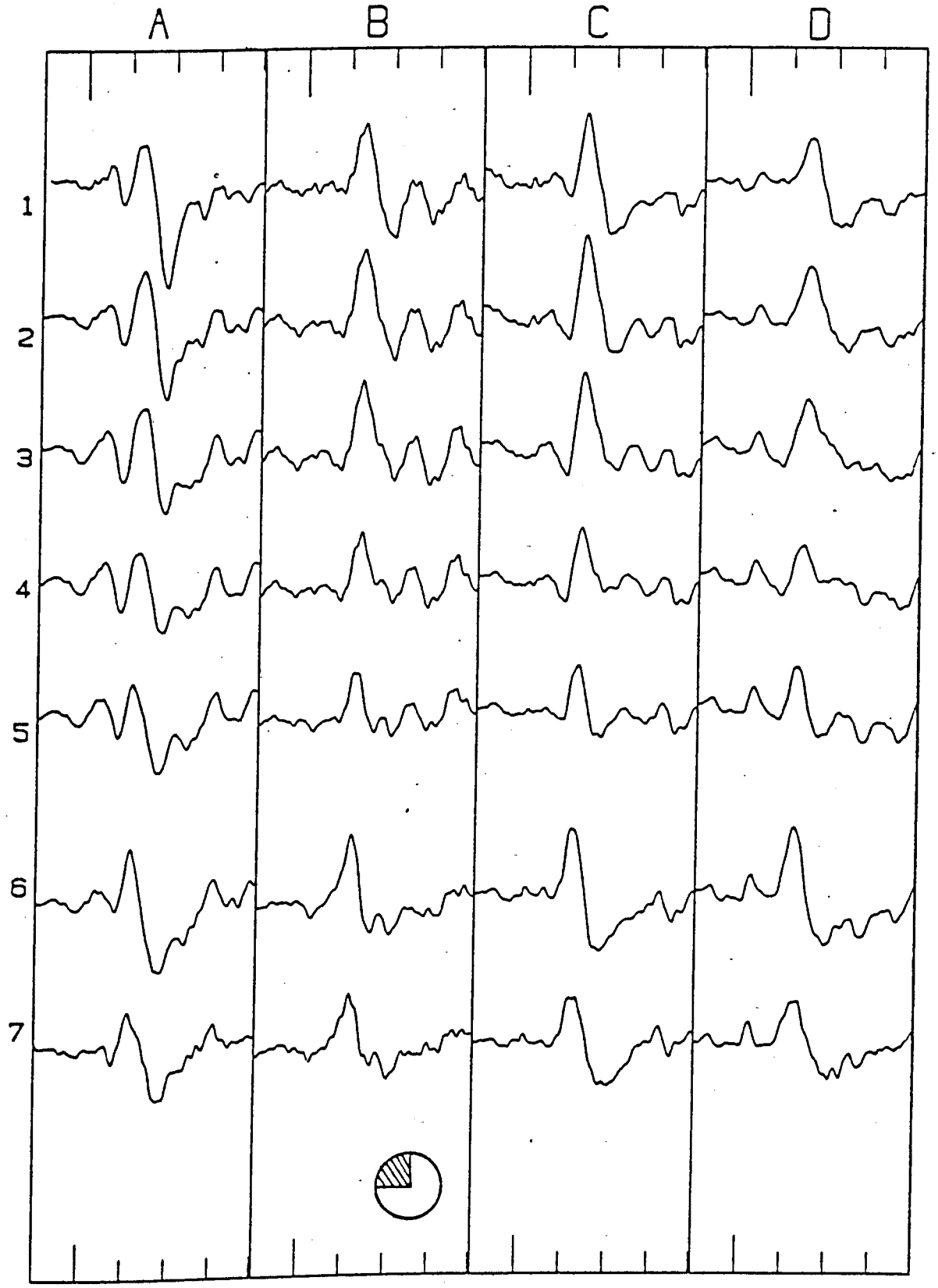


Fig.12.7d

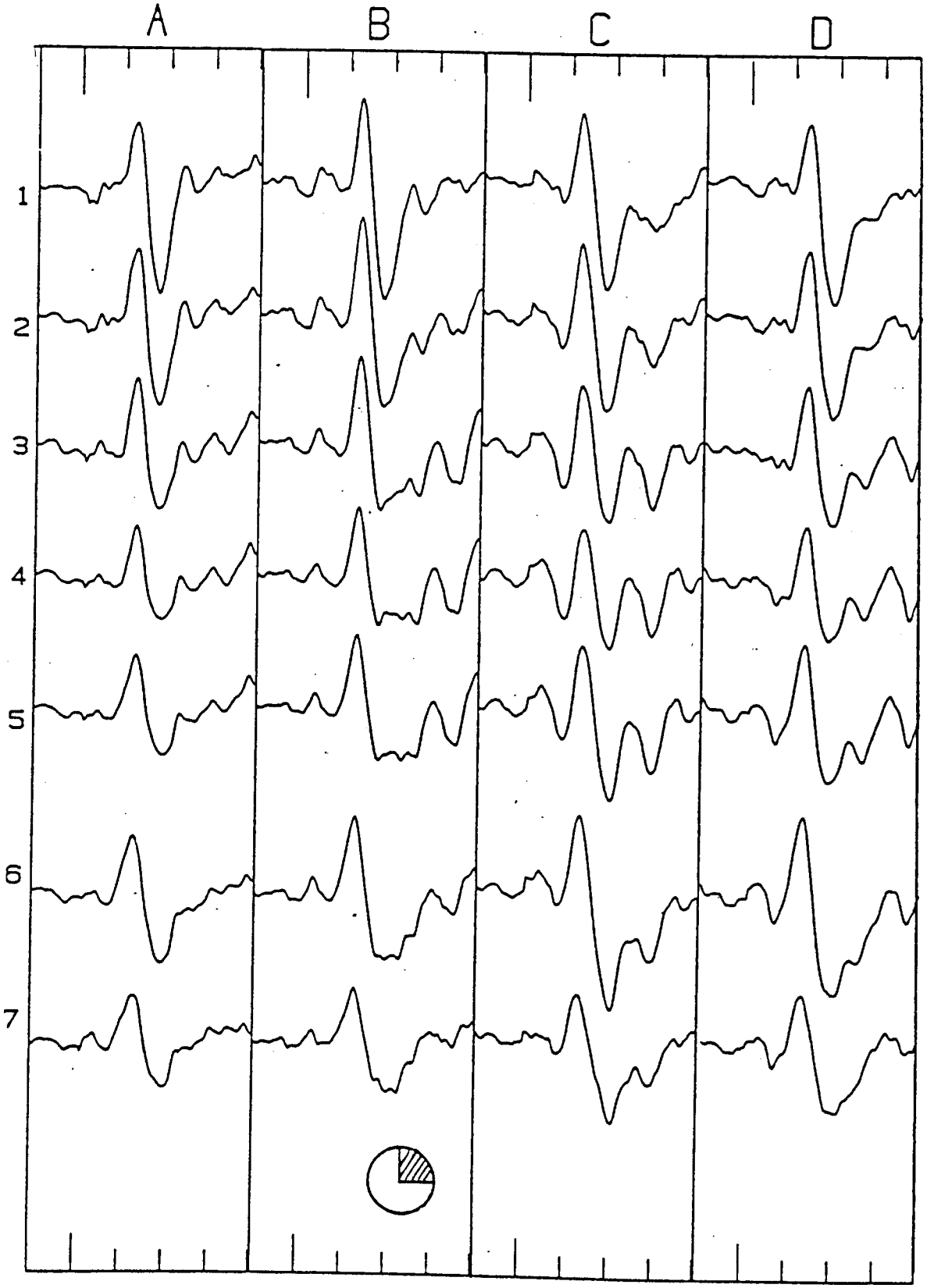


Fig. 12.7e

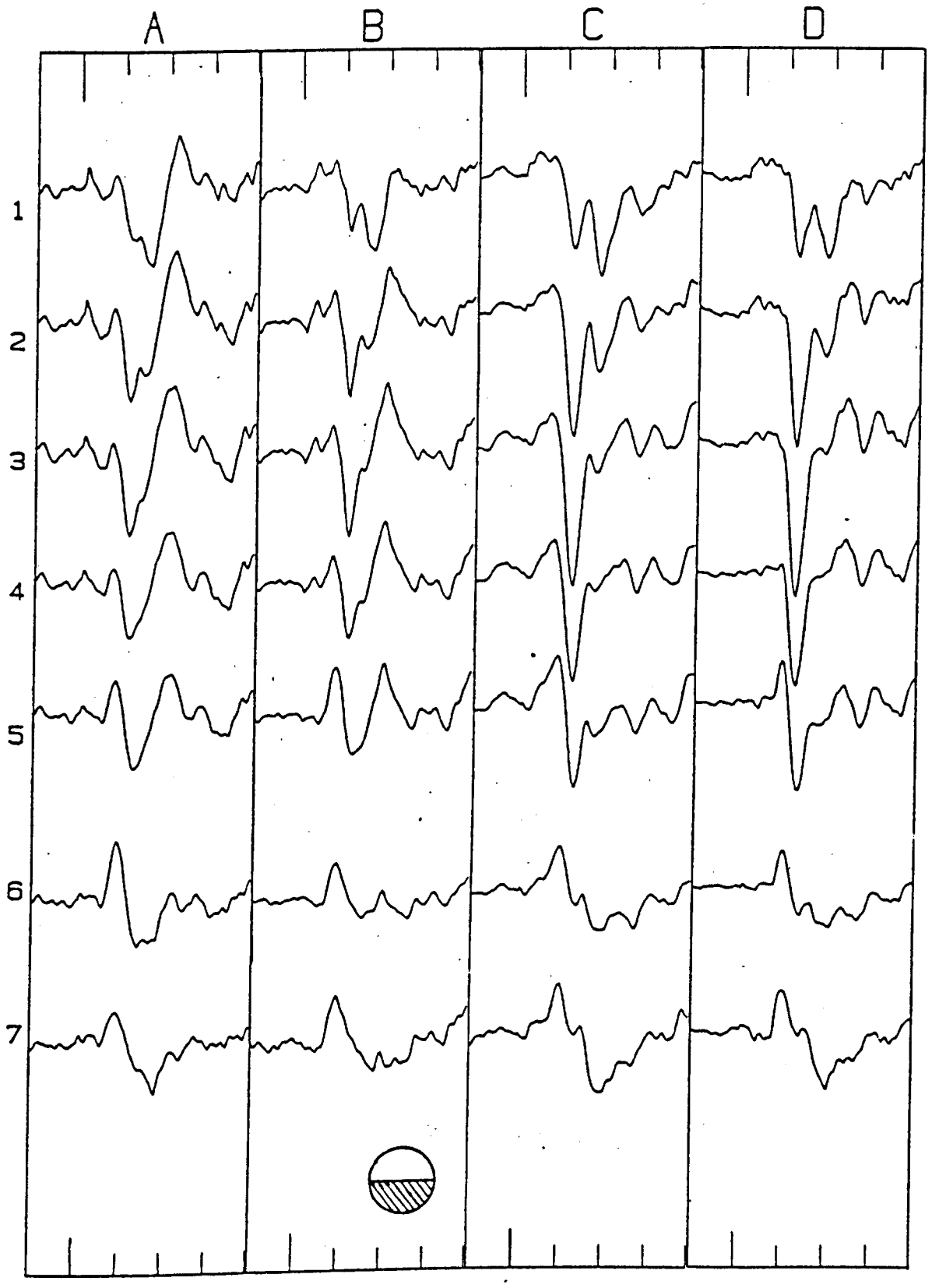


Fig. 12.7f

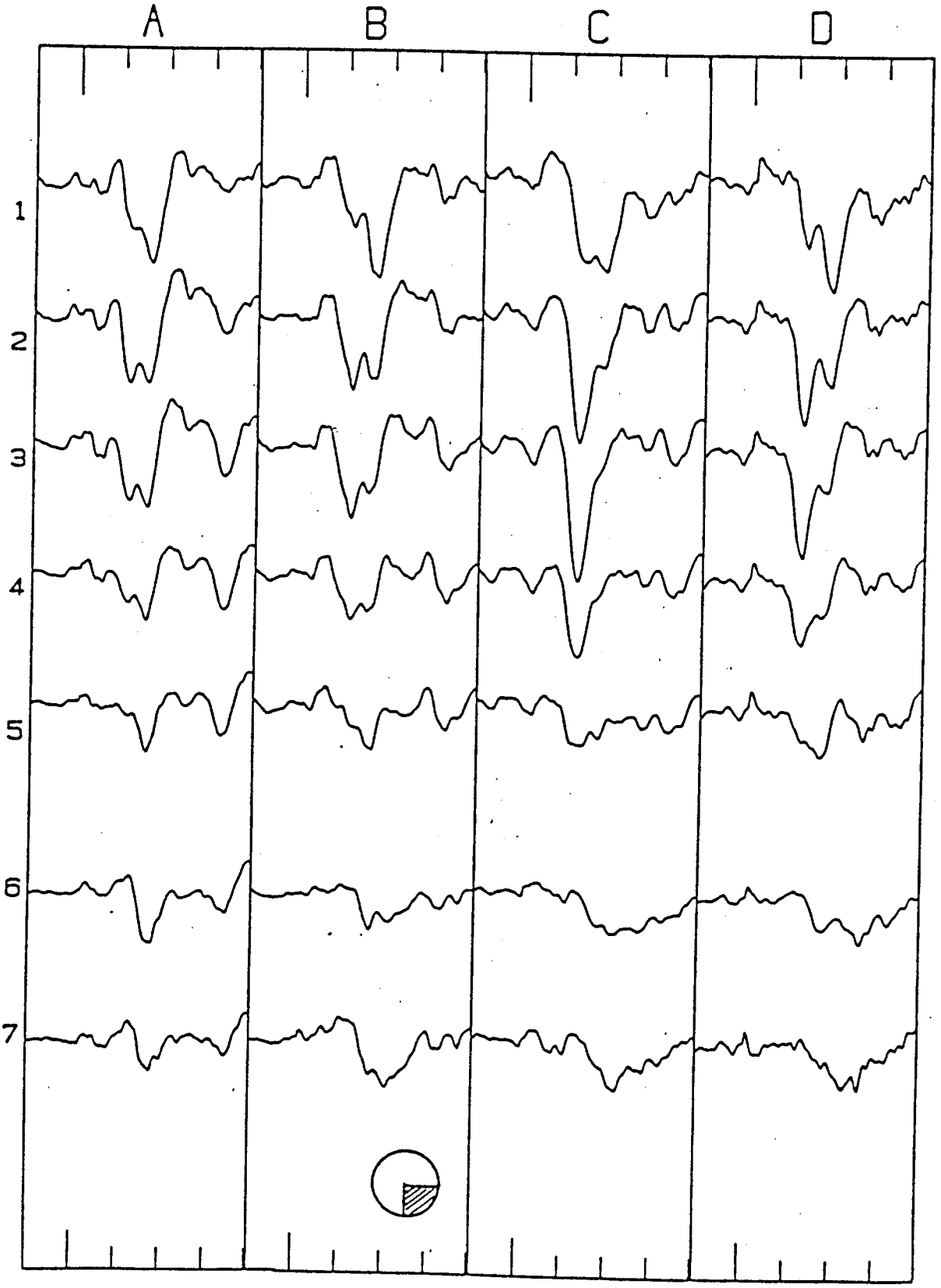


Fig. 12.7g

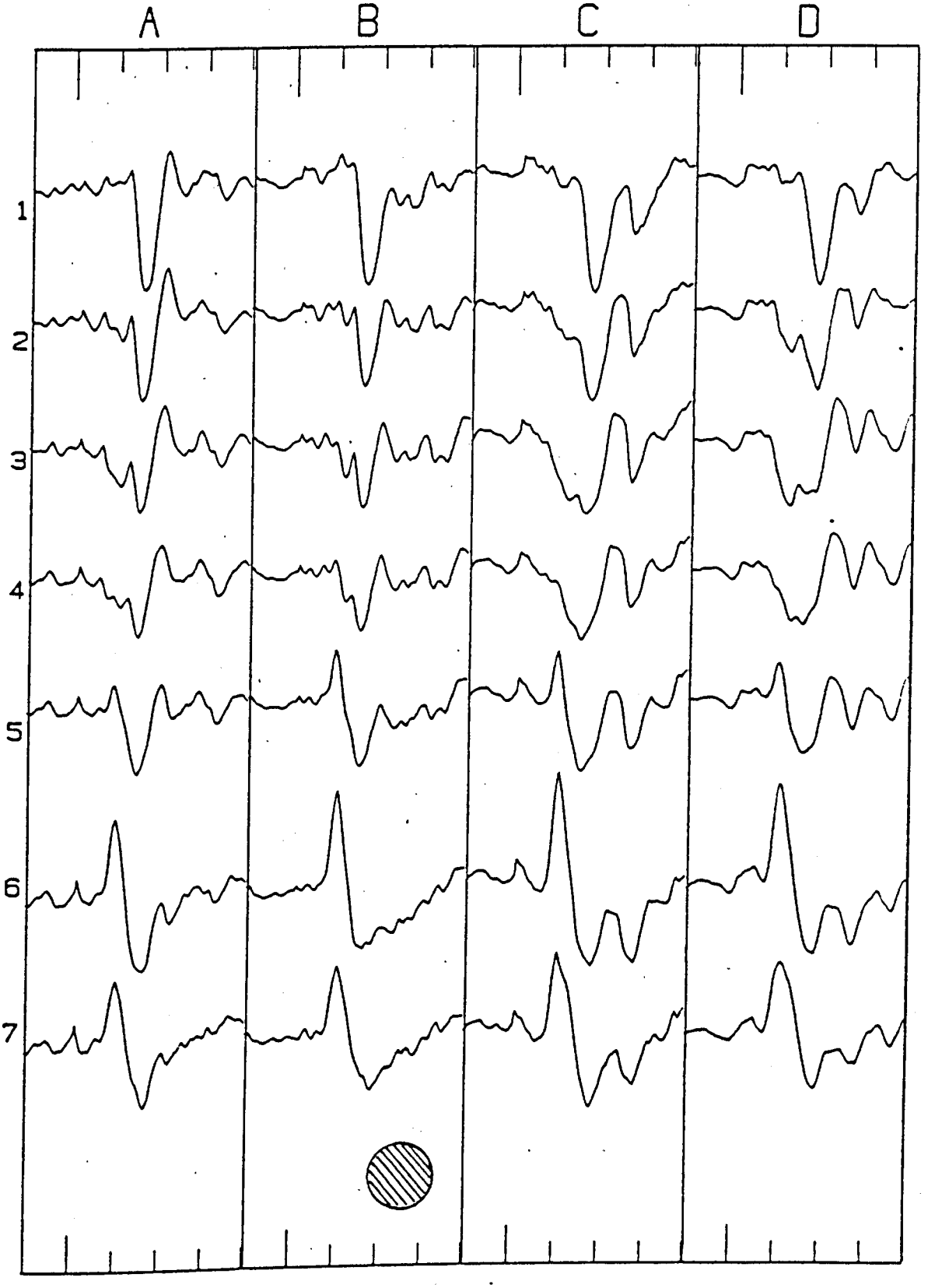


Fig. 12.7i

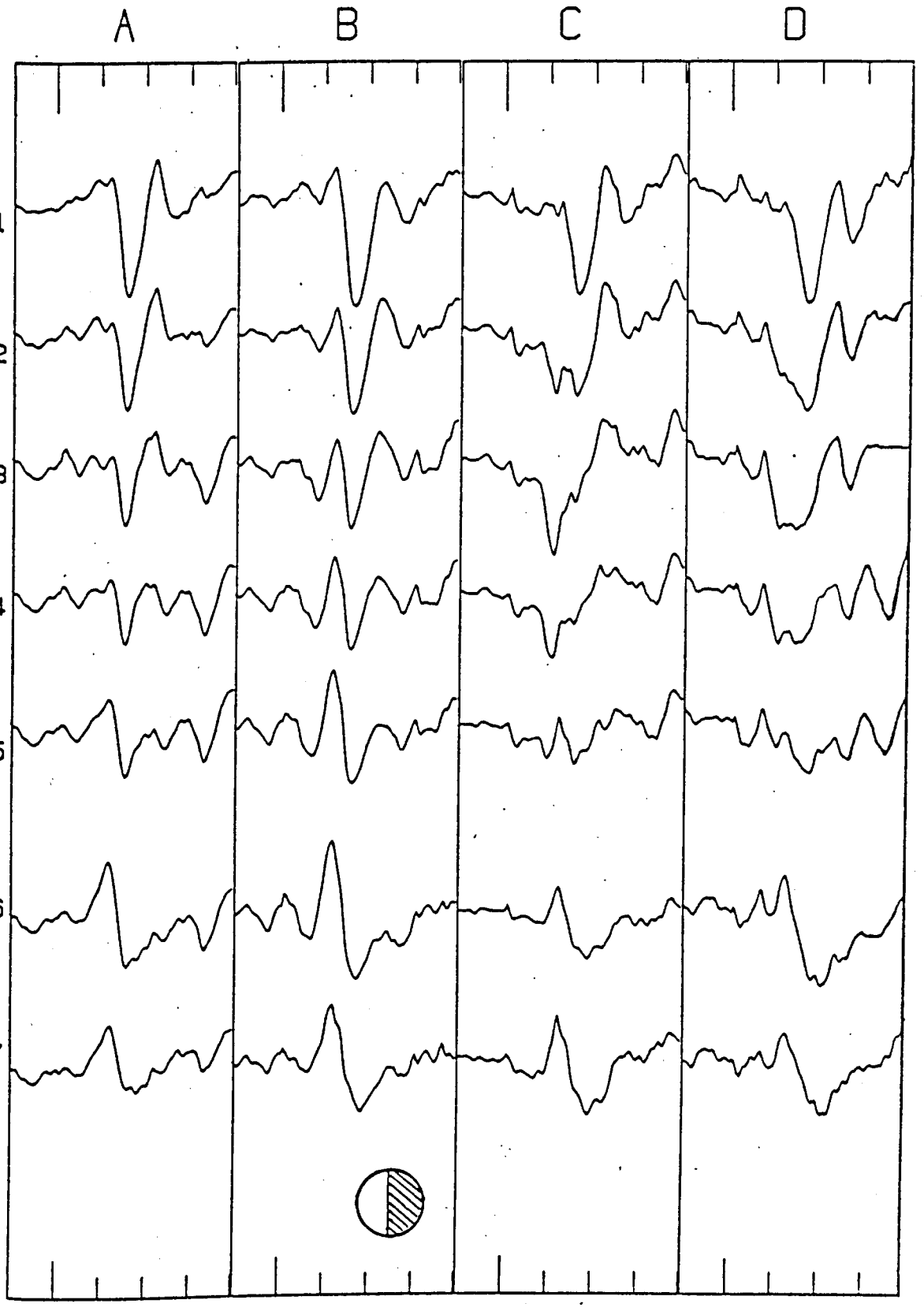


Fig. 12.7j

Figure 12.8

Tranverse amplitude distribtions for the 90-105 msec sample recorded from subject M.J.M. Bipolar placements are at munbers 6 and 7.

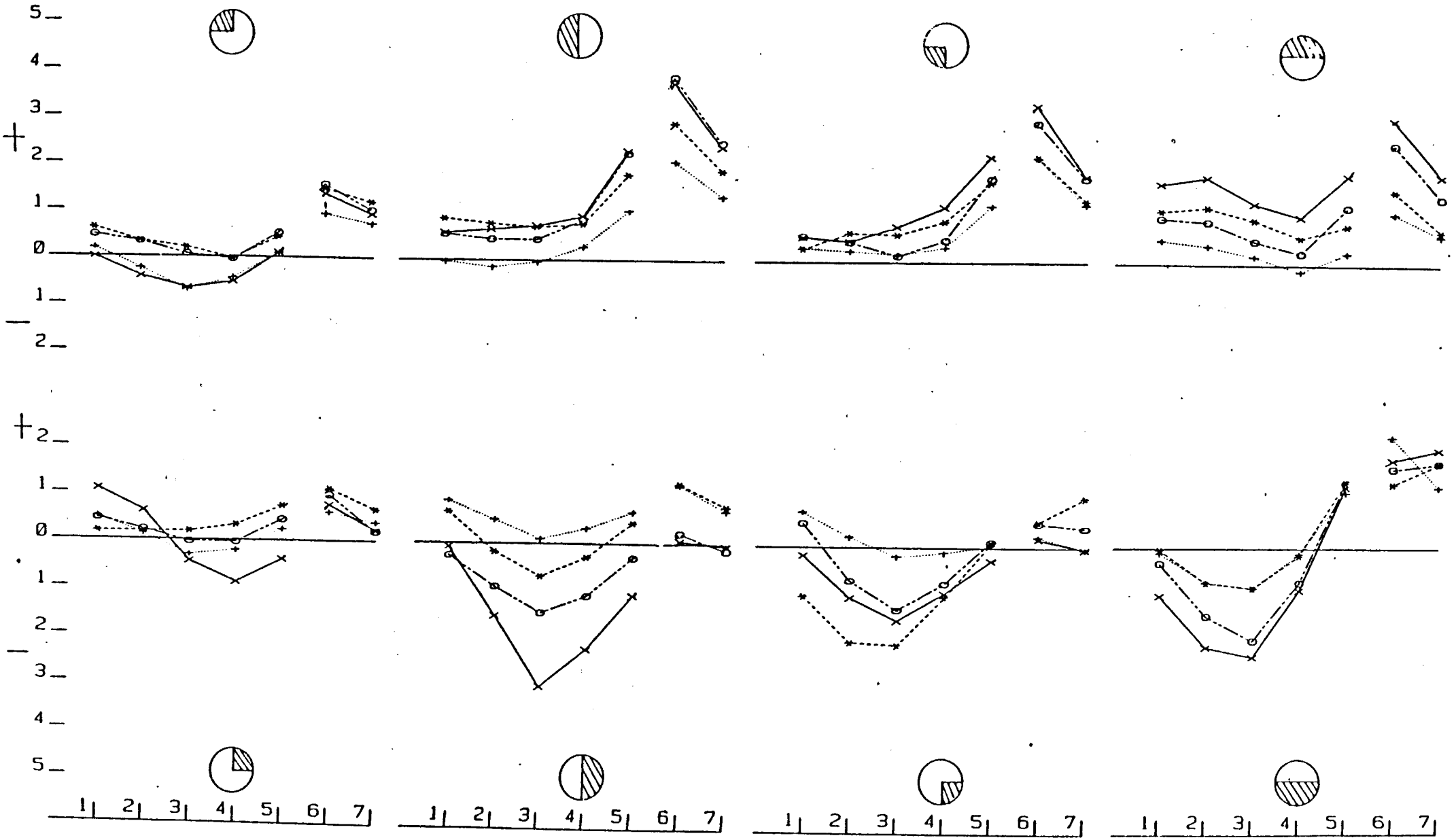
Achromatic luminance contrast =

Monochromatic luminance contrast=

Isoluminant colour contrast=

Colour contrast + 80% trans N.D. filter=

Midline electrode is at number 3.


5
4
3
+
2
1
0
1
2
−
+2
1
0
1
2
3
4
5
−
1 2 3 4 5 6 7
1 2 3 4 5 6 7
1 2 3 4 5 6 7
1 2 3 4 5 6 7

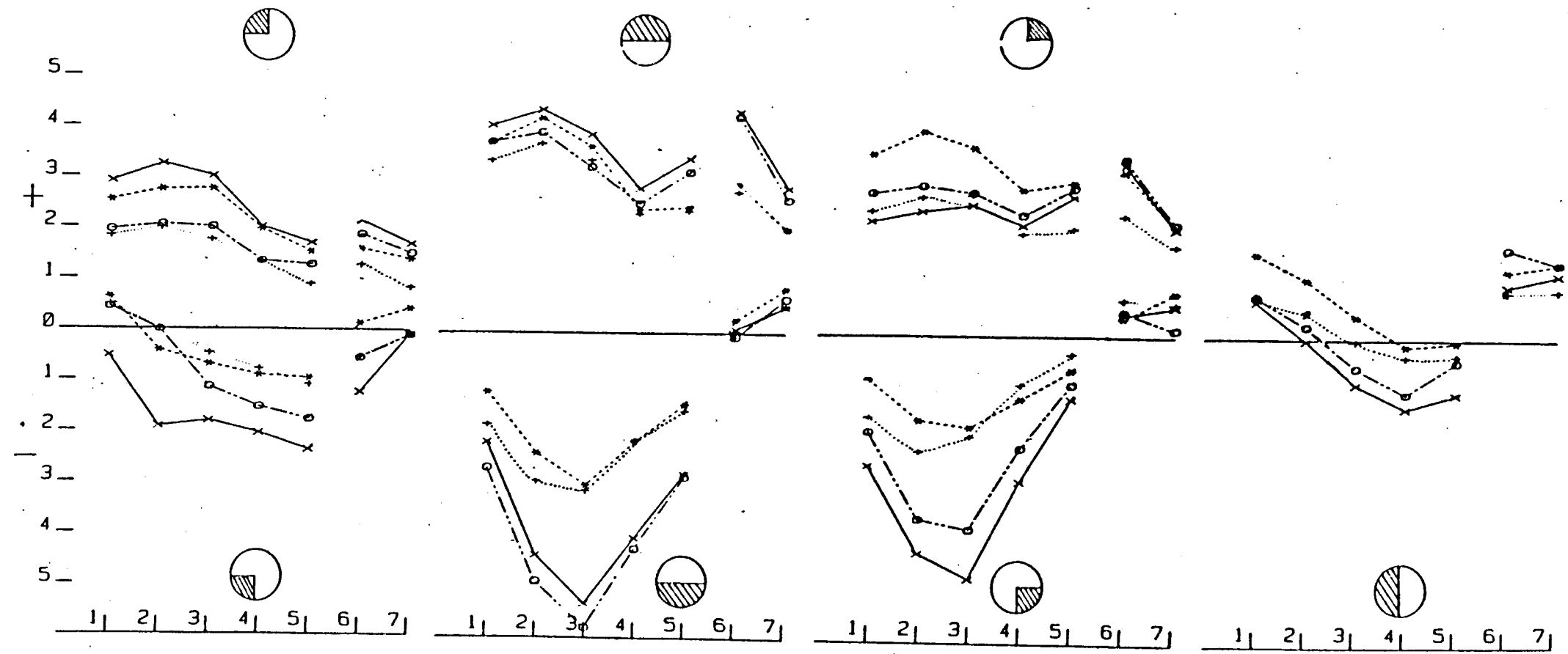
The distribution of activity in this latency range, plotted as a function of pattern retinal location appears to be independent of stimulus type. The data are again consistent with the notion that the mechanisms producing colour contrast VEPs are likely to be located within the same region of cortex as those producing achromatic and monochromatic pattern VEPs. CII:- In figure 12.7c,d,e are shown the responses recorded from upper field and upper left and right quadrant stimulation. The monopolar waveforms show a large positive potential at latency of 110-120 msec (increasing from condition A-C). The distribution of this activity appears consistent across the scalp. A peak of comparable latency but opposite polarity is evident in the response to lower half field stimulation, (figure 12.7f). A similar peak is evident in the waveforms produced with lower left quadrant stimulation, (figure 12.7b.). The picture is complicated here, however, by the fact that at this pattern (retinal) location the peak of 90-102 msec latency is also maximal in amplitude and will thus temporally overlap with CII. Also evident in the waveforms recorded with lower half-field stimulation is a negative potential of a latency of 160-182 msec which appears to interact with the CII peak. This activity will be considered in greater detail below.

In figure 12.9 the distribution of activity at latencies between 109-120 msec are plotted (electrode positions 6 and 7 are bipolar placements). Whilst there are slight differences in amplitude at any one particular electrode site, the overall distribution for each of the four conditions is similar. Within this latency range, upper field activity is all positive, lower field responses all negative, consistent with previous data and with the model of Jeffreys & Axford (1972b).

The negative activity in the latency range between 160-180 msec appears to be localised to electrode positions 1 and 2. The peak is particularly evident with lower half and lower left quadrant field stimulation, figures 12.7f & b respectively and the degree of electrode localisation is apparently dependent on stimulus conditions, see figure 12.7h. With upper field stimulation a negative peak of a similar latency is also evident on the trailing edge of the large positive CII component. Again, this peak is of a greater amplitude at electrode positions 1 and 2, and since the latency of this activity is similar in both upper and lower half field reponses; this negative peak (now termed N160-180) may reflect activity from the same cortical source. However the absence of polarity reversal suggest this source is not

Figure 12.9

Transverse amplitude distribution of the 109-120 msec sample. Conditions as for figure 12.8.



located in a retinotopically organised region of visual cortex.

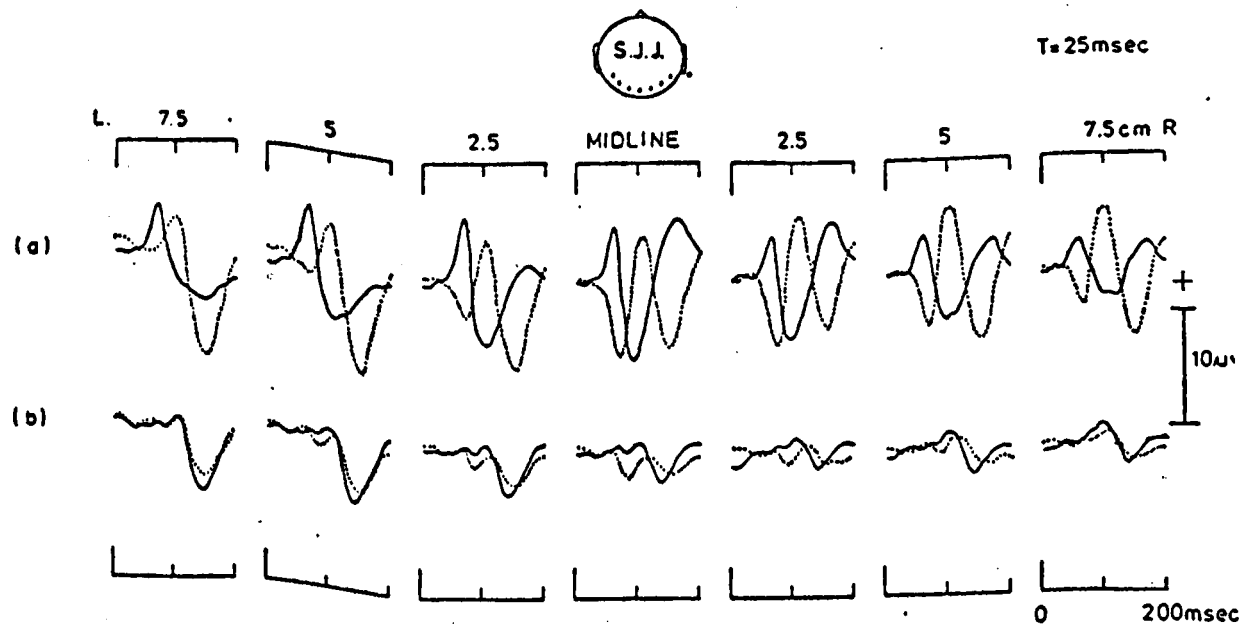
For this subject, since CII reverses polarity for upper and lower half-field stimulation full field stimulation should produce potential cancellation, which would, isolate the N160-180 peak, particularly at electrodes 1 and 2. In figure 12.7(i) are shown the VEPs elicited by full field stimulation and it is clear that the above does indeed occur. [The large positive potential evident at electrodes 6 and 7 is CI as shown in chapter 9]. The 'isolation' of this N160-180 peak at the the eccentric electrodes over the left occipital can also be seen in the responses recorded from the right half field, shown in figure 12.5j.

If the N150-180 peak is indeed a component, as defined by Jeffreys (1980), it would appear that it is generated in a non-retinotopically organised region of cortex unlike those pattern specific components, (see figure 12.10). It is difficult from the present data to determine whether the N160-180 reflects either pattern specific activity or whether it reflects non-pattern specific activity similar to the N150 component, which can be observed in the large field pattern-onset responses as shown in figure 12.10.

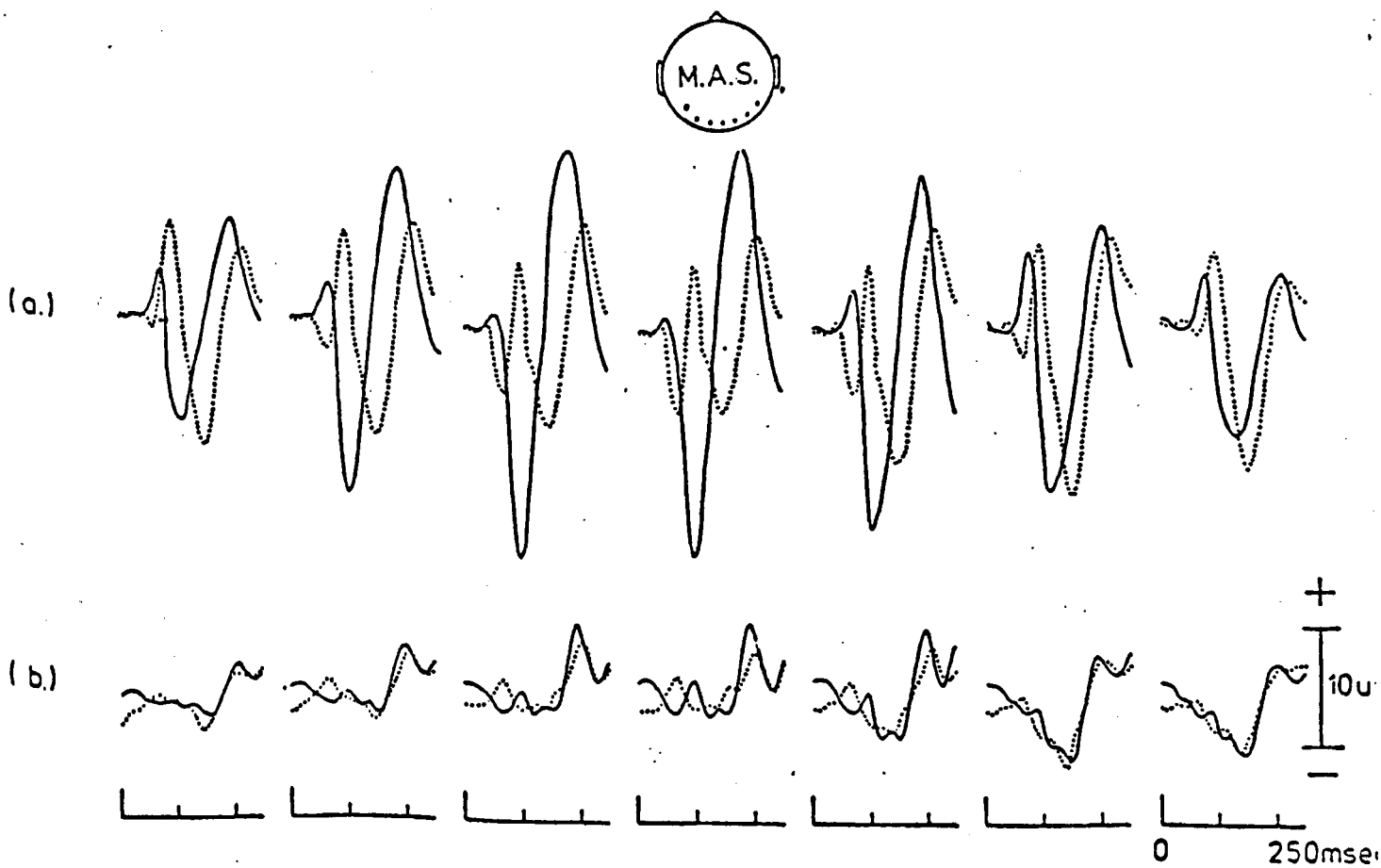
Jeffreys (personal communication) has found that although non -pattern specific components do not show polarity reversal as a function of stimulus location their distribution over the scalp is often asymmetrical, as shown in the above figure. These VEPs may therefore be generated in regions of cortex lying outside the visual areas. In contrast to luminance-related activity the amplitude of these late, non-pattern speific components appear to be independent of the overall change in mean luminance or contrast (when pattern stimulation is used). It is possible therefore that this N160-180 activity is in fact the so called non-pattern specific peak N-150 rather than some 'new' and as yet unidentified component. To examine this prediction in detail the following experiment was undertaken.

12.4:- A comparison of the scalp distribution of patterned, non-patterned luminance and colour contrast VEPs. Transverse mapping.

In this experiment a transverse row of electrodes was again used. In this case however all recording was monopolar, with reference to the right ear; the actual position of each electrode and the spacing between then has been given in figure 12.1a. Because the N160-180



LOWER (—) AND UPPER (—) HALF-FIELD VEPs TO (a) ISOLATED SQUARES AND (b) N.D. FILTER STIMULI



Lower (——) and upper (·····) half-field VEPs to (a) chequerboard and (b) n.d. filter stimuli.

Figure 12.10
From Jeffreys (unpublished data).

appears most pronounced at electrodes over the left hemisphere, the electrode distribution was therefore asymetrical. The electrode numbering will not therefore correspond to that used in the previous transverse distribution, but equivalent placements can easily obtained.

The plan of this experiment was to repeat some of the conditions of the previous experiment; in this case limited to the monochromatic luminance contrast and isoluminant colour contrast conditions, to provide a more comprehensive monopolar distribution. Where necessary, bipolar responses were obtained by computer subtraction of any two monopolar channels.

Pattern evoked responses were then compared to three conditions of non-pattern stimulation which were as follows:-

A:- total change in mean luminance in the absence of any change in chromaticity, produced by occluding the green field.

B:- isoluminant colour stimulation.

C:- ditto, with the addition of 80% transmission neutral density filter placed in the green field, to produce a combined luminance and chromatic contrast pattern.

The object of these conditions was to determine the pattern specificity of the N160-180 component.

For comparison between the responses obtained in these experiments and those previously reported, the following table can be used to obtain comparable electrode positions.

This study :-	1	2	3	4	5	6	7	8
Previous :-	-	-	1	2	3	4	5	-

Results and Discussion

Contrast specific activity:- In figures 12.11a-d the monochromatic luminance and isoluminant colour contrast responses have been superimposed. These figures illustrate that the only major difference between the response elicited by these types of stimulation is the longer peak latency of the VEP produced by colour contrast stimulation, the amplitude is similar in each case. The actual latency difference is some 15 msec for each component.

In figure 12.11a are shown the waveforms elicited by upper half and upper quadrant field stimulation. Consistent with the data of the preceding experiment, the waveforms are dominated by a large positive component of peak latency 108-109 msec for monochromatric luminance

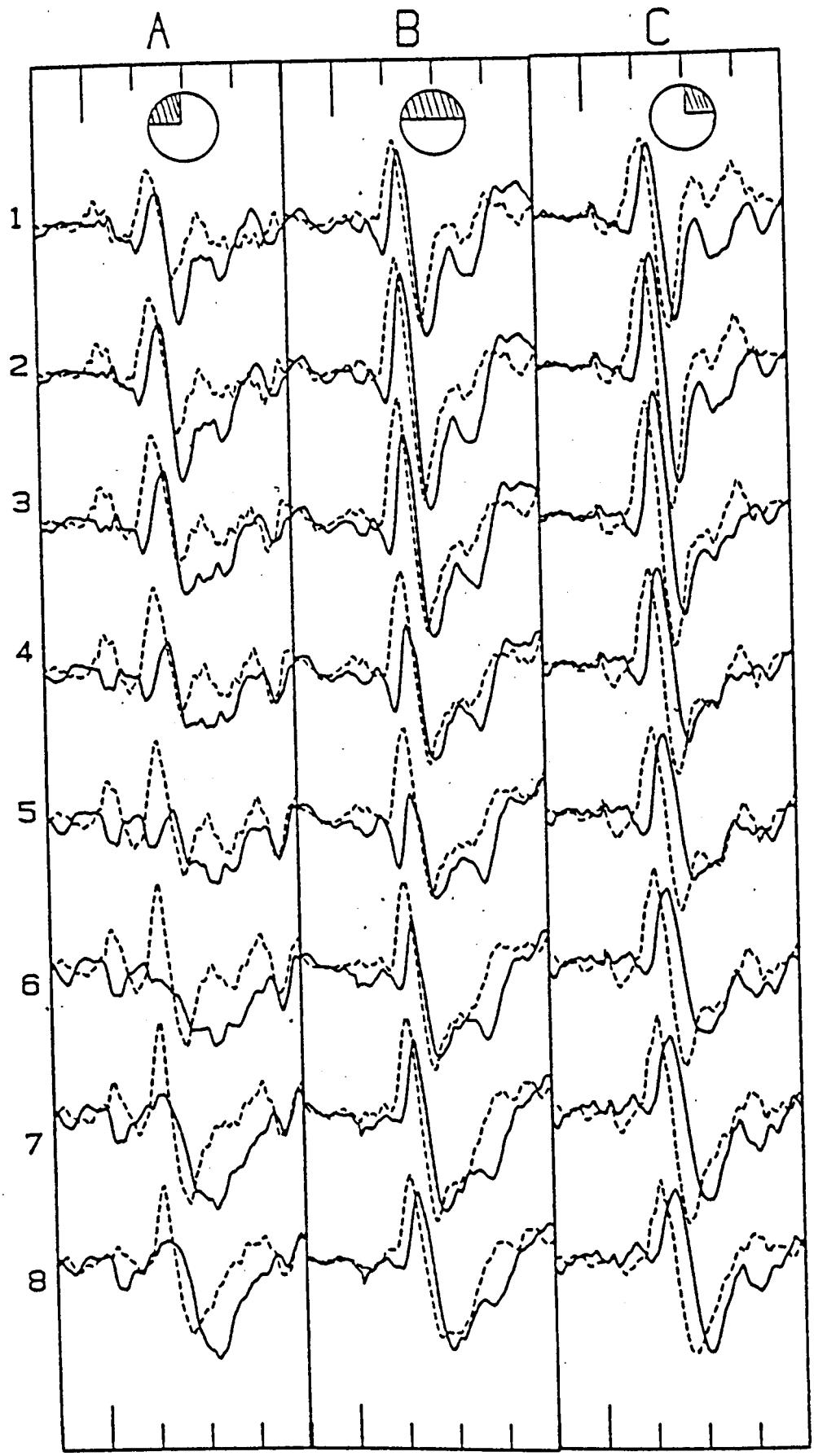


Figure 12.11

Monoplar VEPs elicited by monochromatic luminance contrast (dashed trace) and isoluminant colour contrast (continuous trace).

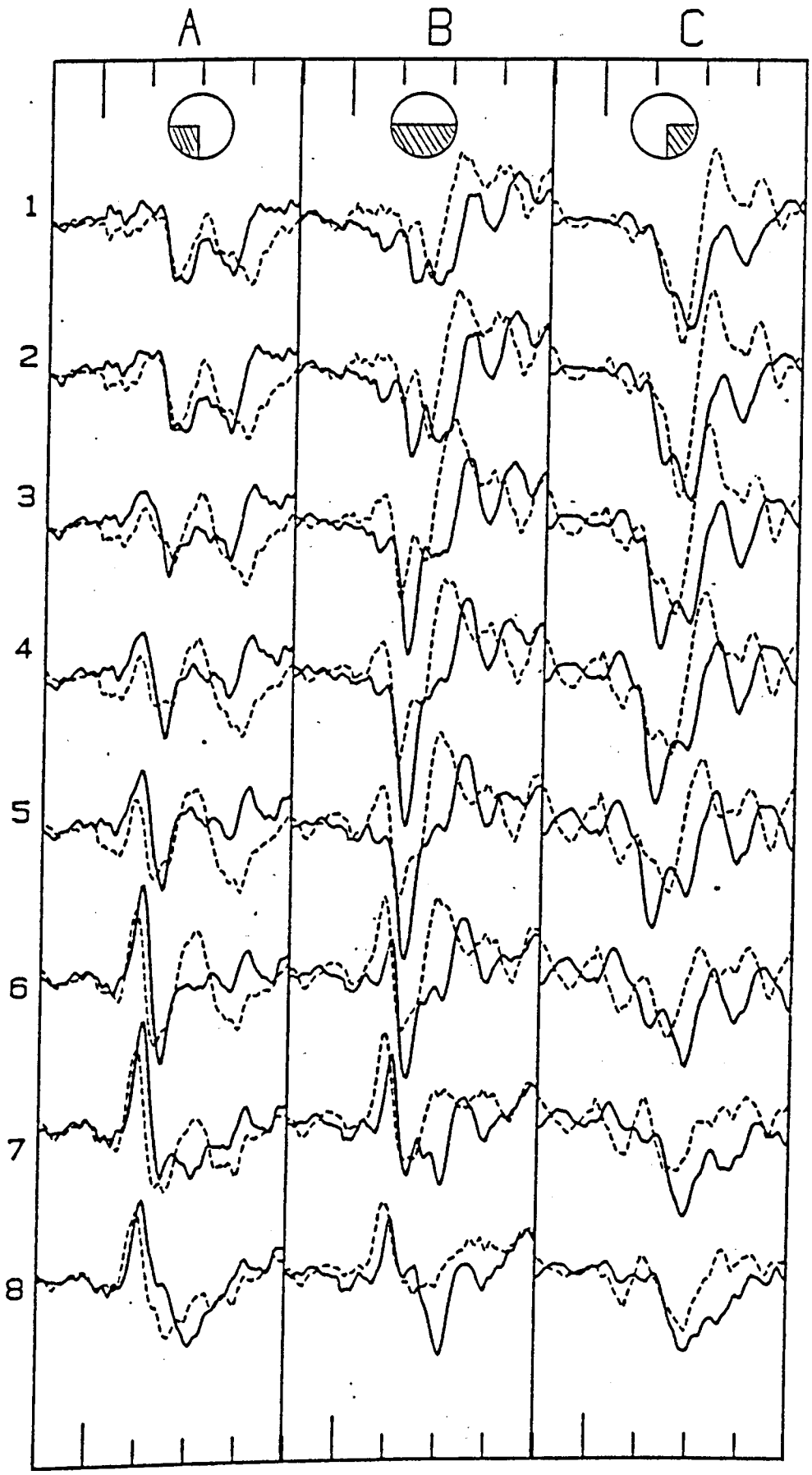


Figure 12.11b

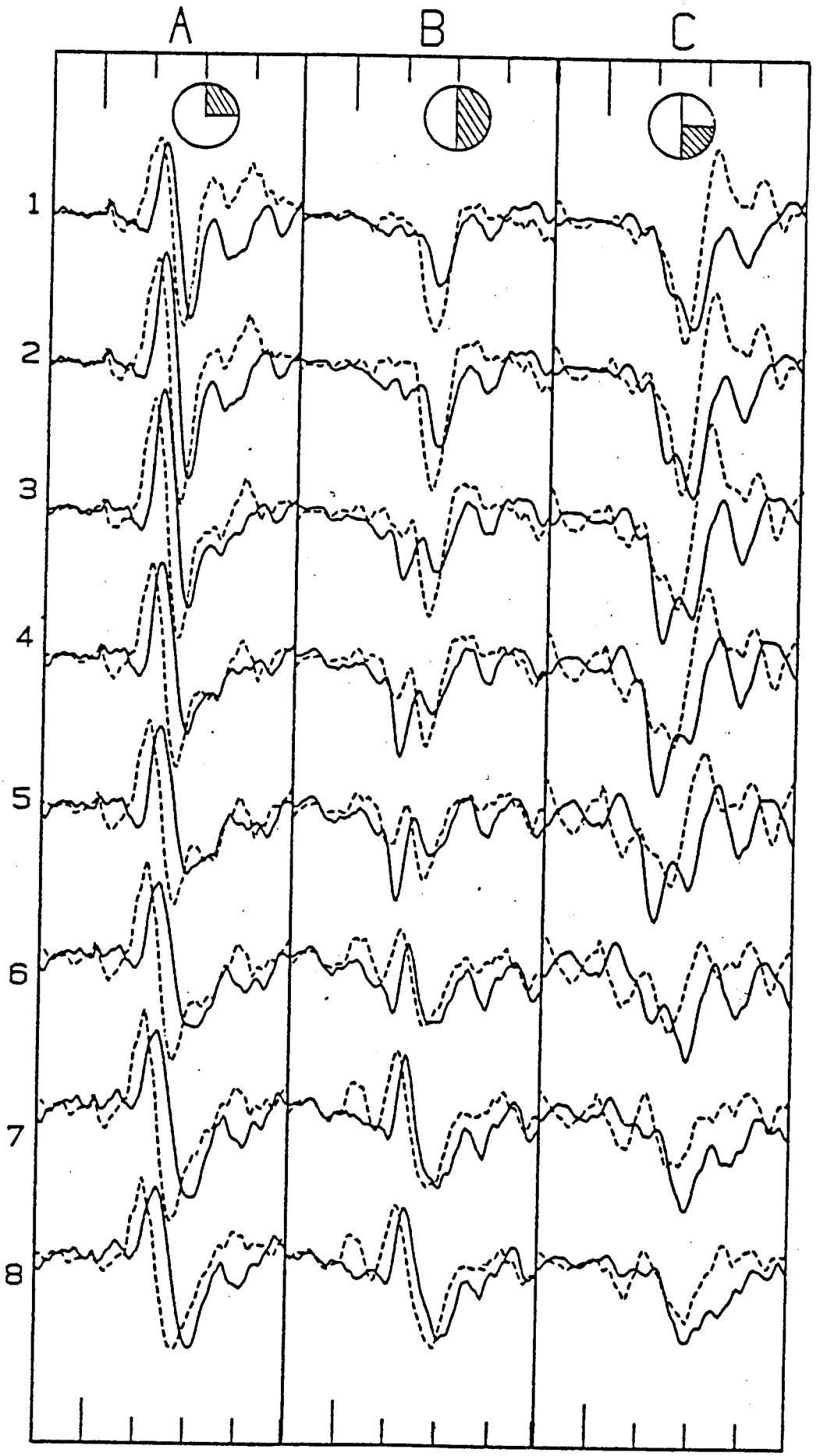


Figure 12.11c

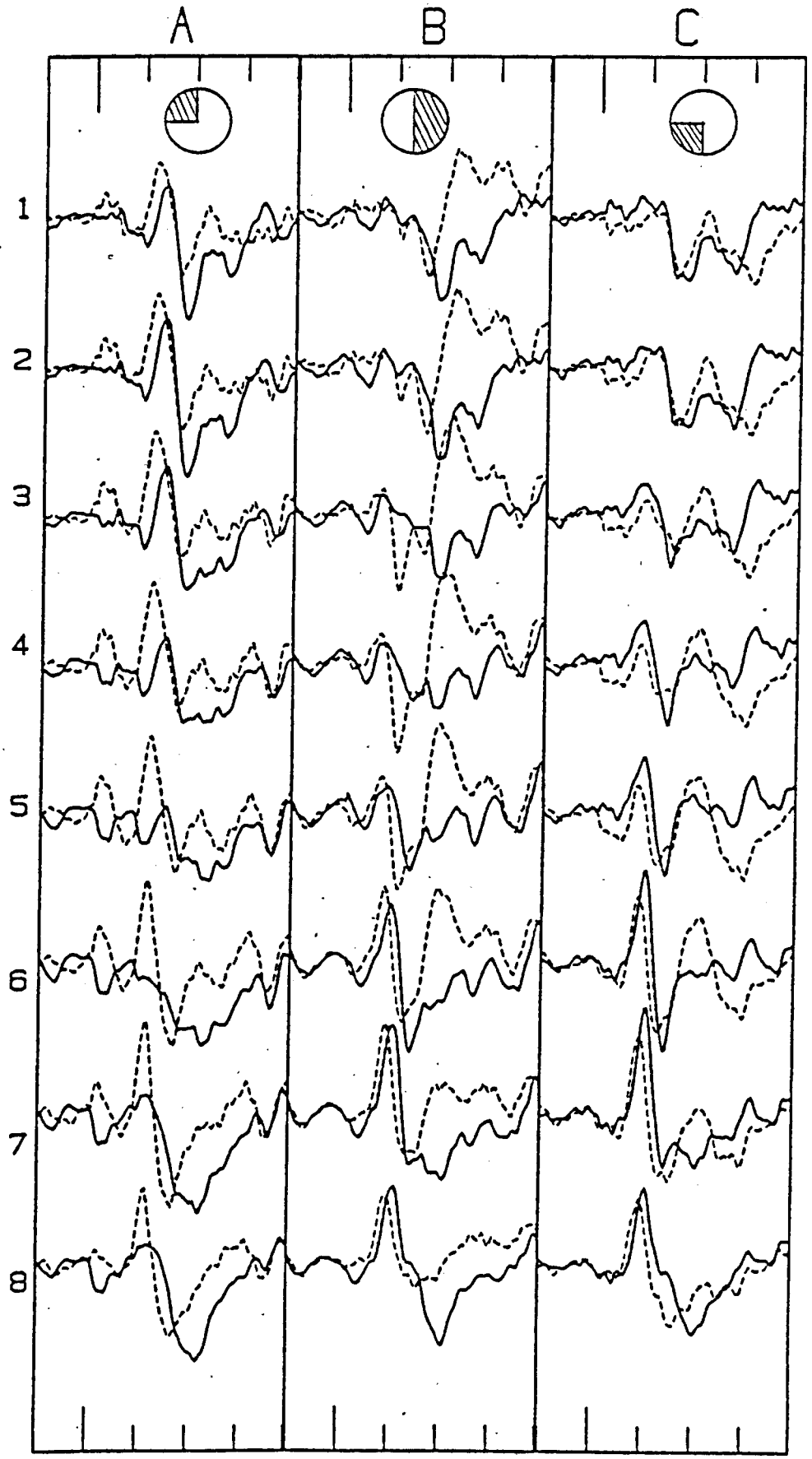


Figure 12.11d

contrast and 118-123 msec for colour contrast conditions. A negative peak with similar latency is evident in the waveforms obtained with lower half-field stimulation, which is in this case maximal at the midline electrodes, 3 and 5, (see figure 12).11b. In the waveform obtained with lower left quadrant field stimulation, this negative potential is less clearly identified. This could be explained by the occurrence of a large positive potential with a contralateral maximum which has a peak latency of 92-95 msec for monochromatic luminance contrast, and a latency of between 105-108 msec for colour contrast stimulation.

The upper and lower field polarity reversal of the peak at latencies of 108-120 msec (both conditions) is also consistent with the previous study and reflects the activity of CII. In the latter portion of the waveform a more complex pattern of activity is observed for, in addition to the major pattern specific components, there is evidence of a negative potential with a maximum at the eccentric electrodes over the left occiput. This peak is clearly illustrated in the responses obtained to right field and lower right quadrant stimulation (shown in figure 12.11c), where for the latter, it appears to combine with the negative CII at the contralateral electrodes to form a broad peak. As CII is maximal at and near the midline, this N160-180 peak will appear to separate out.

The N160-180 peak appears less evident in the waveforms obtained to monochromatic luminance contrast stimulation, apparently because there is a broad positive potential with a contralateral maximum under these conditions. It is possible that this peak is CIII but in the present subject this component cannot be reliably identified (Jeffreys personal communication).

The N160-180 component is most clearly identified in the responses to right half-field stimulation, particularly at the contralateral electrodes. It is clear that the CII component which is of opposite polarity for upper and lower field stimulation has, under these conditions, cancelled. However, because of the non-symmetrical distribution of CII elicited by lower field stimulation, the extent of this potential cancellation will vary. Thus at the most eccentric ipsilateral electrodes, there is a single positive potential whose peak latency is similar to that of the positive potential recorded to upper right quadrant stimulation.

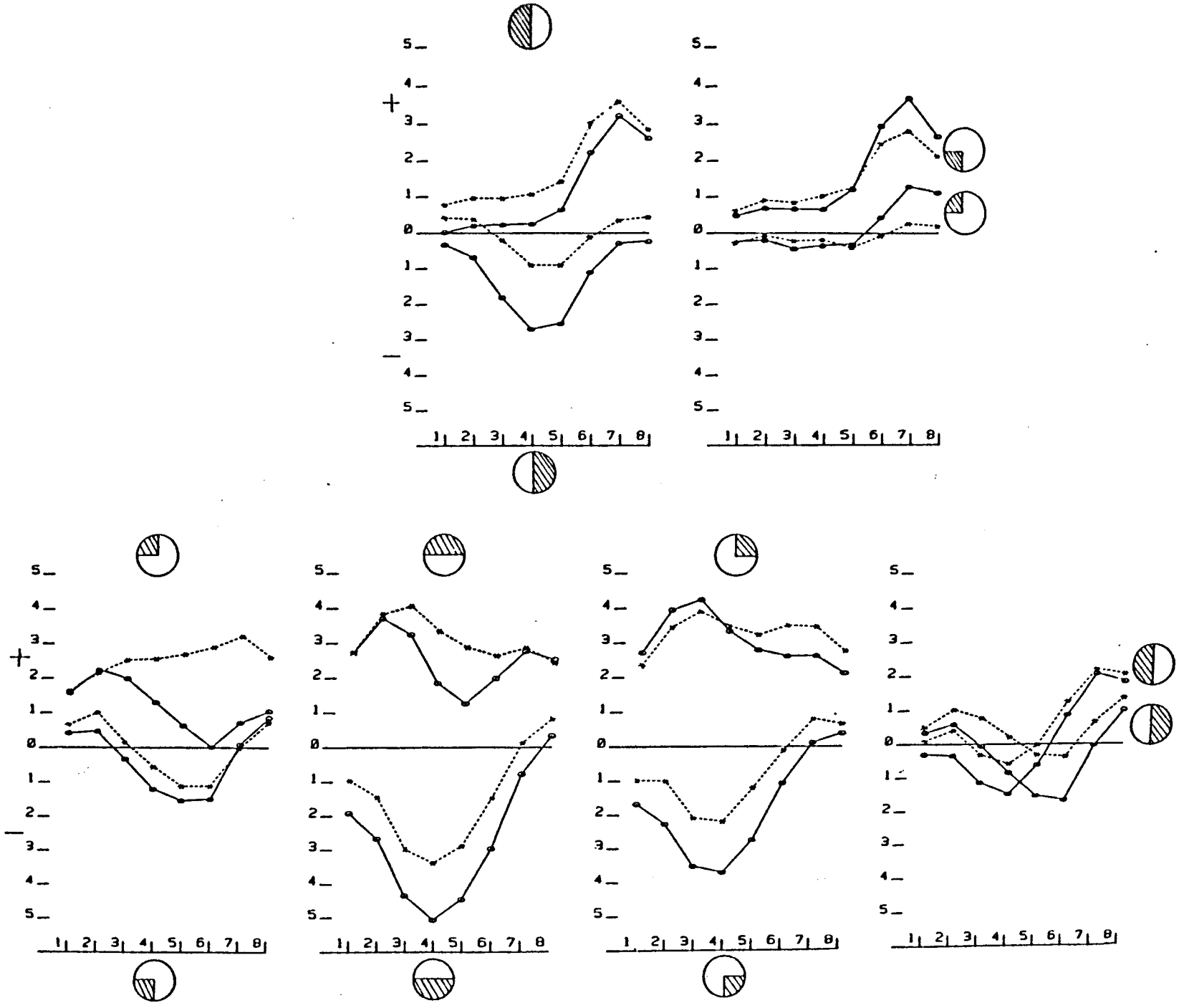
Figure 12.12

Top two graphs illustrate the amplitude distribution of the 90-105 msec sample.

Bottom four graphs illustrate the amplitude distribution of the 110-120 msec sample.

Monochromatic luminance contrast = ✳------✳----✳

Isoluminant colour contrast = O———O———O


5 4 3 2 1 0 1 2 3 4 5
1 2 3 4 5 6 7 8

In figure 12.12 are shown the distribution of activity at a latency comparable to that of CII. The distributions are similar to that reported in the previous transverse mappings and indicate that the two types of pattern stimulation produce activity of comparable amplitude at each electrode site thus suggesting that they are generated in the same region of visual cortex. At the top of figure 12.12 are illustrated the amplitude distributions of the 90-103 msec sample, for left field and lower and upper left quadrant-field stimulation.

The conclusions to be drawn thus far are

A:- that the results are consistent with the previous transverse surface mapping and suggest that isoluminant colour contrast stimuli produce little modification to the overall distribution of pattern evoked activity.

B:- that there is no evidence of a specific component unique to isoluminant colour contrast stimulation.

Whilst the N160-180 peak is again found in these waveforms, and tends to be of greater amplitude for colour contrast as opposed to luminance contrast, it is, nevertheless, evident in the response to the latter and it would appear unlikely that it is produced by some region of visual cortex specifically sensitive to colour contrast. However the absence of polarity reversal as a function of opposing half-field stimulation might be consistent with the prediction that it is generated in an area such as V4, the evidence is merely suggestive and the alternative explanation which is that this peak reflects non -pattern specific activity, appears a more likely one. In the light of the following evidence the latter suggestion appears to be confirmed.

Figure 12.13a & b show upper half field and lower half field responses together with respective quadrant responses for non-patterned stimulation. Compared with the waveforms produced by patterned stimuli, these VEPs vary little as a function of retinal location. Moreover, there is little evidence of any variation between the three types of non-patterned stimulation in disagreement therefore with the studies of Ciganek (1969) which report such differences between VEPs elicited by patternless fields varying in luminance and colour. The major differences appear to be ones of amplitude and there no evidence to suggest any characteristic waveform associated with any particular type of stimulation.

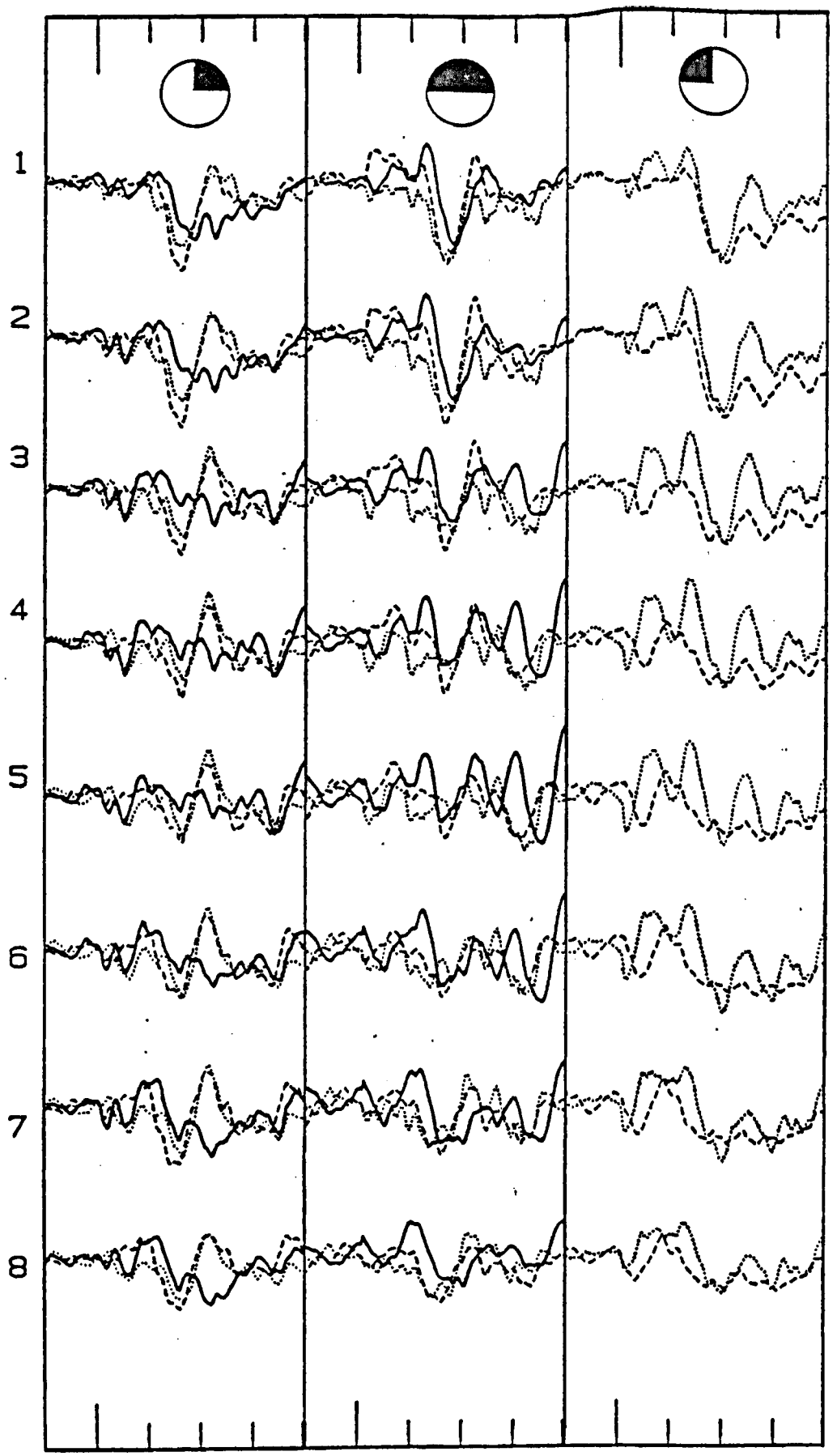


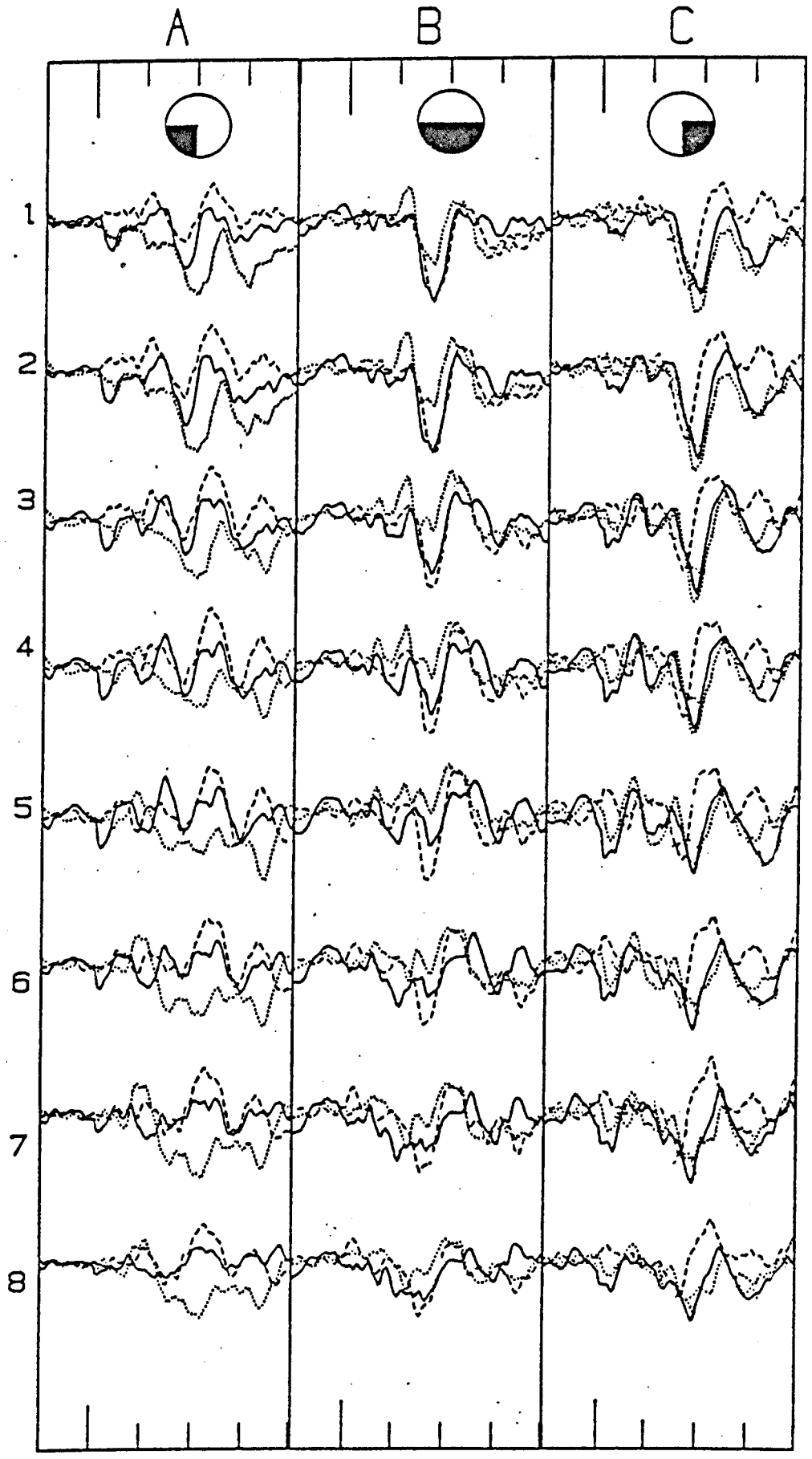
Figure 12.13a,b

VEPs elicited by unpatterned stimulation of upper (12.13a) or lower (12.13b) half-field.

Dashed trace:- 100% change in luminance.

Dotted trace:- Combined 30% reduction in luminance and change of wavelength.

Full trace:- Isoluminant change in wavelength.


A
B
C
1
2
3
4
5
6
7
8

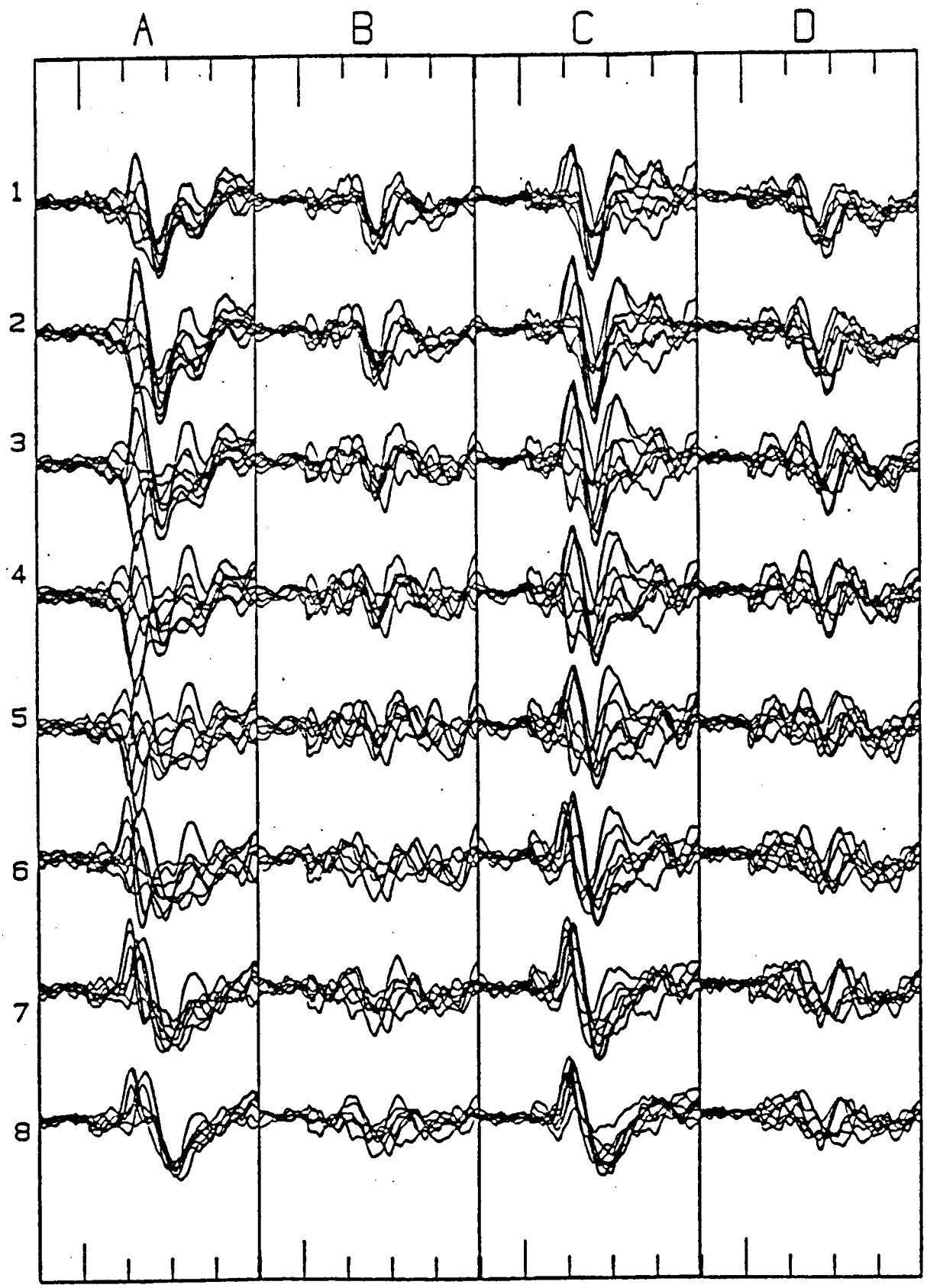


Figure 12.14

Superimposed half-field and quadrant VEPs, for two types of patterned and unpatterned stimulation.

Column A:- Isoluminant colour contrast
Column B:- Unpatterned change in wavelength.
Column C:- Monchromatic patterned contrast.
Column D:- 100% Luminance change.
Numbers refer to electrode locations in figure 12.1.D.

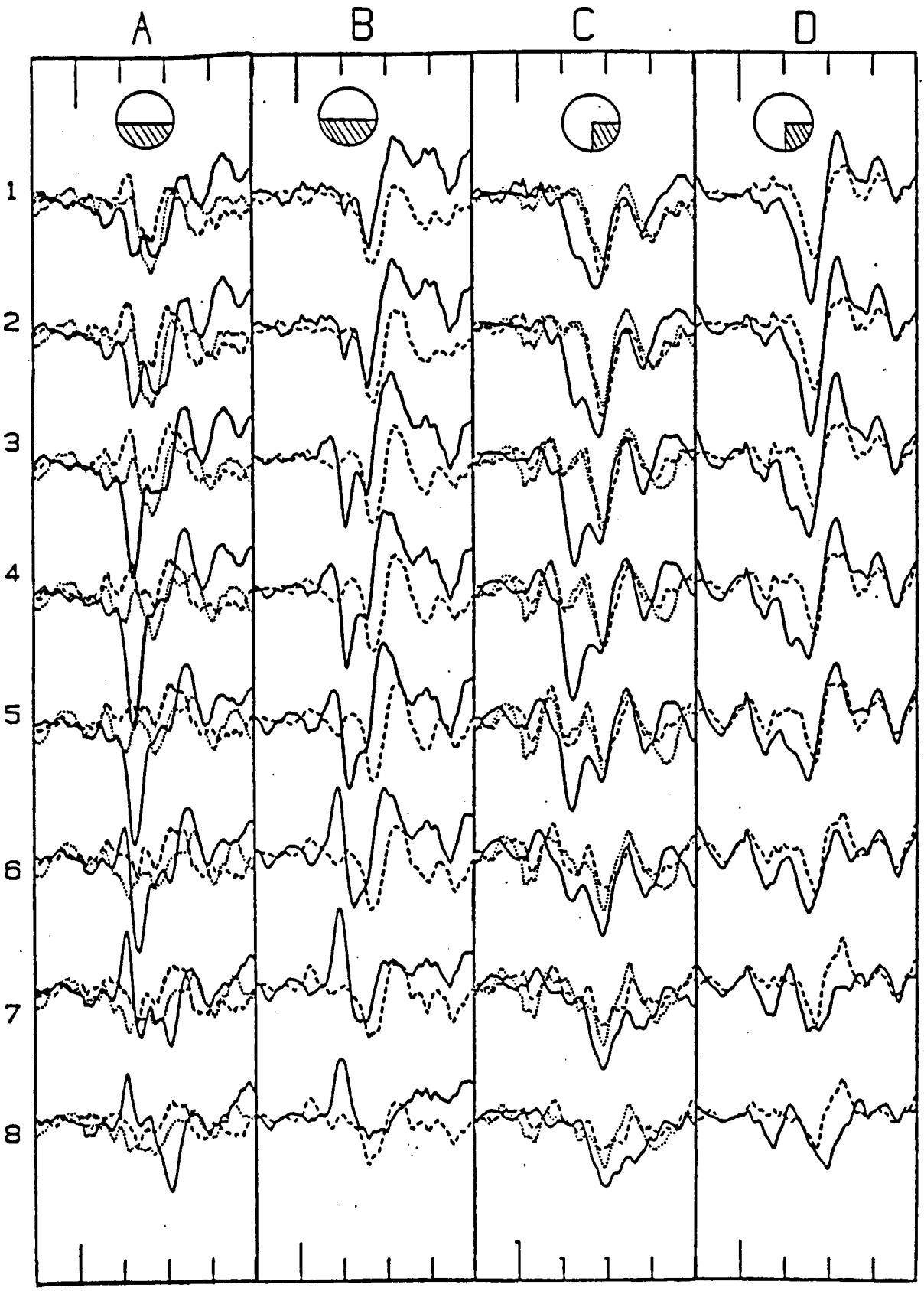


Figure 12.14b

Superimposed VEPs elicited by patterned and unpatterned stimulation.

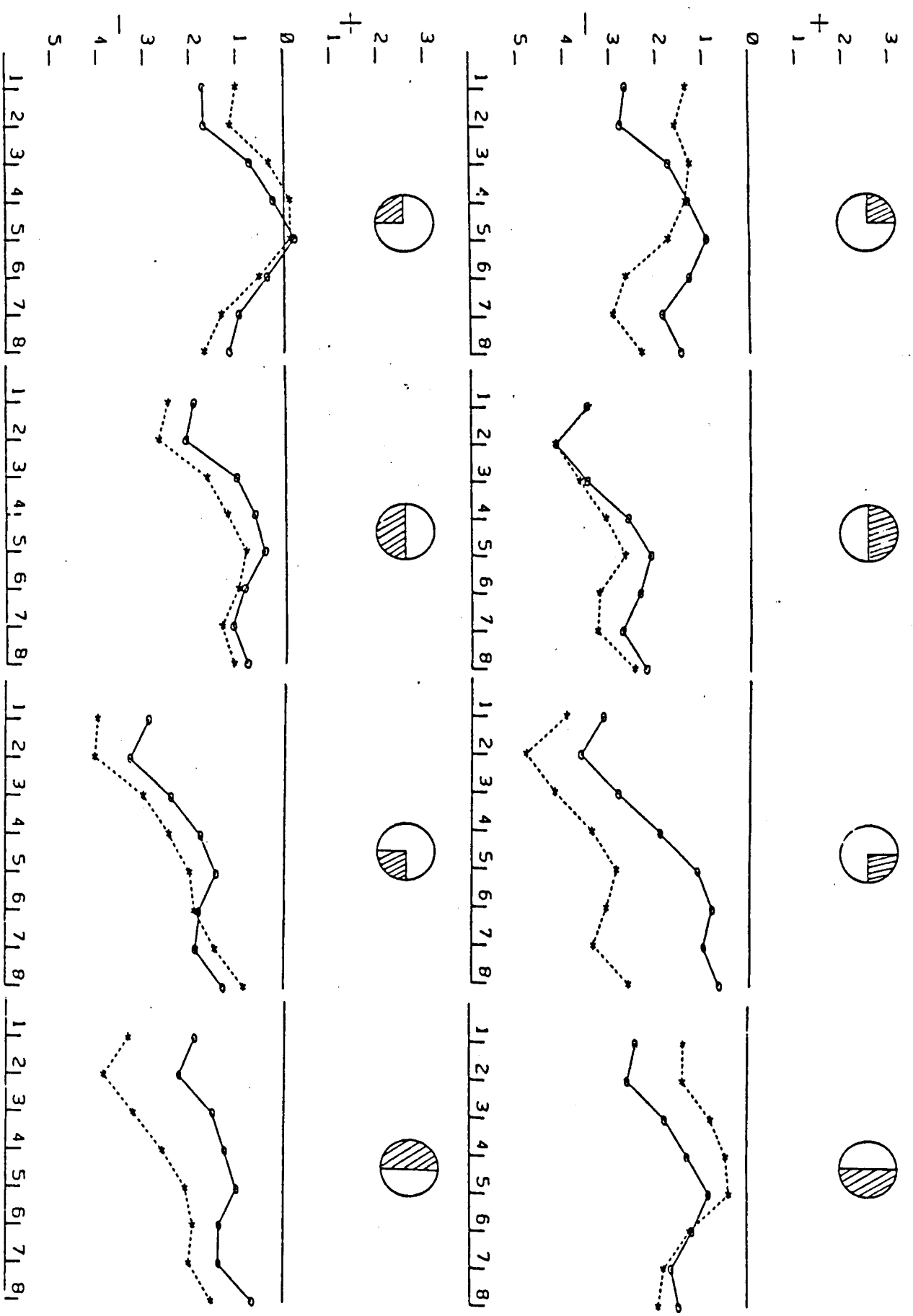
Column A:- Full trace isoluminant colour contrast.
Dashed trace wavelength change + 30% reduction in luminance.
Dotted trace isoluminant change in wavelength.

Column B:- Full trace monochromatic luminance contrast.
Dashed trace 100% luminance change.

Waveforms in column C as for column A; column D as for column B.

Figure 12.15a

Amplitude distibution of the 160-180 msec sample. Dotted trace is for monochromatic luminance contrast, full trace for isoluminant colour contast.



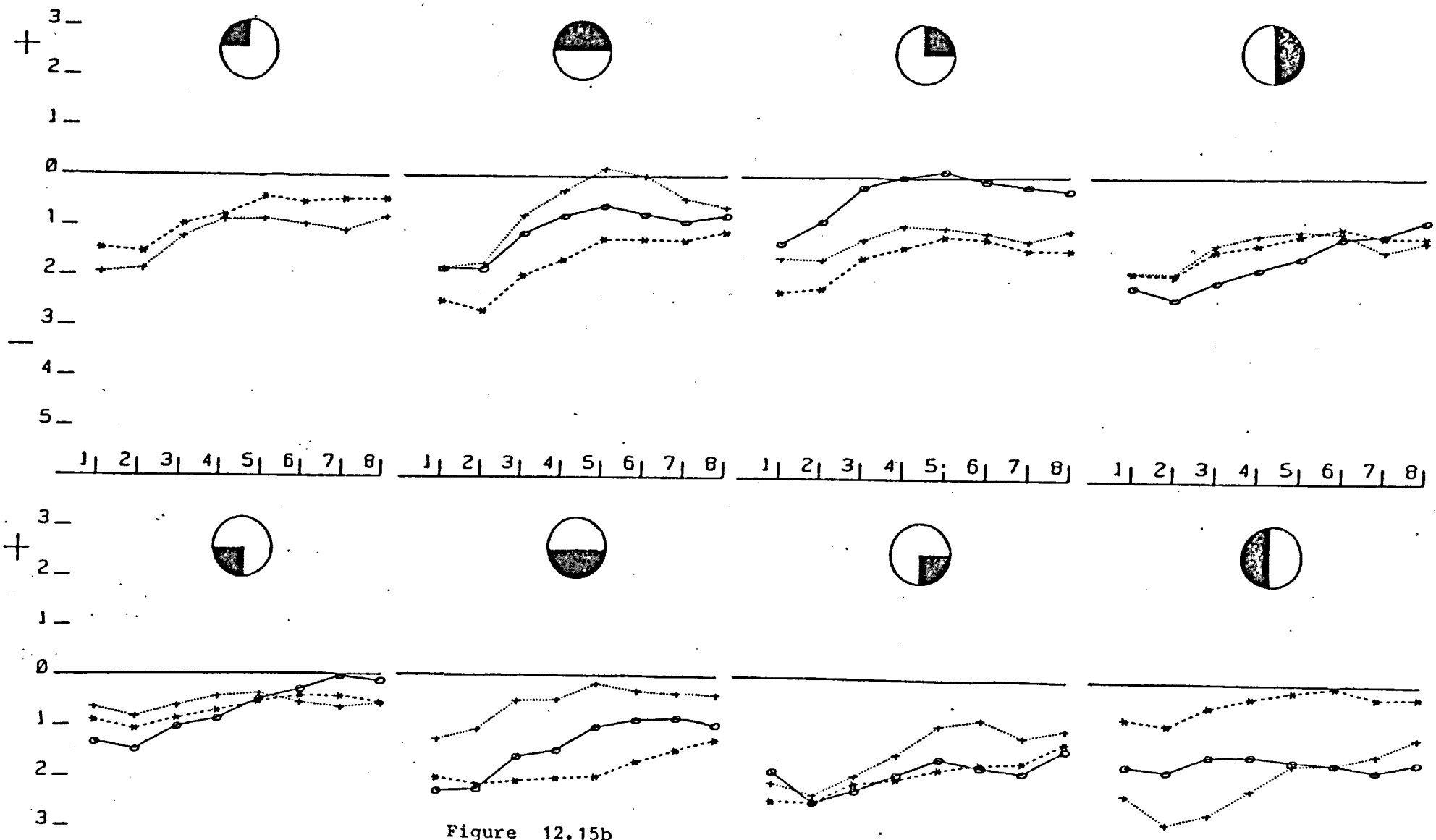


Figure 12.15b

Amplitude distribution of the 160-180 msec sample for three type of unpatterned stimulation.

These non-pattern specific VEPs differ from pattern specific ones in having a polarity entirely independent of retinal location, as is clearly illustrated in figure 12.14a, where in each of the four columns are superimposed, for one specific condition, the reponses obtained to the stimulation of each half field and quadrant. Pattern specific activity is maximal at around 90-130 msec after stimulus onset, (see column A & C), whilst activity evoked by structureless stimuli occurs some 130-180 msec after stimulus onset (column B & D).

The important aspect of these non-pattern evoked waveforms is that the major activity is a negative peak at a latency of 160-180 msec which again has a maximum at the left hand side electrodes, and so corresponding to the N150 component (see Jeffreys and Musselwhite, in prep). It appears that this peak is produced by all types of stimulation, patterned and non-patterned, and accounts for the occurrence of the negative potential of peak latency 160-180 msec identified in the previous experiments. This is confirmed in figures 12.14b where the waveforms obtained to pattern stimulation of the lower half and lower right quadrant-field are superimposed on the non-patterned evoked waveforms. The secondary negative peak, evident on the trailing edge of CII and maximal at the eccentric electrodes in the VEPs elicited by patterned stimuli, coincides with the negative peak (160-180 msec latency) in the waveforms produced by patternless stimuli.

In figure 12.15a & b are shown the amplitude distribution for the 160-180 msec sample elicited by both pattern appearance (colour or luminance contrast) and the three types of non-pattern stimulation. These distribution are very similar in showing a maximum over the left occiput which is independent of the stimulus retinal location, and type.

12.5:- General Discussion

There are two main conclusions that can be drawn from these experiments, they are:-

A:- That luminance contrast and isoluminant colour contrast stimuli give rise to a similar distributions of scalp activity.

B:- There appear to be no obvious pattern or indeed non-pattern related VEPs uniquely associated with colour or colour contrast

Figure 12.16

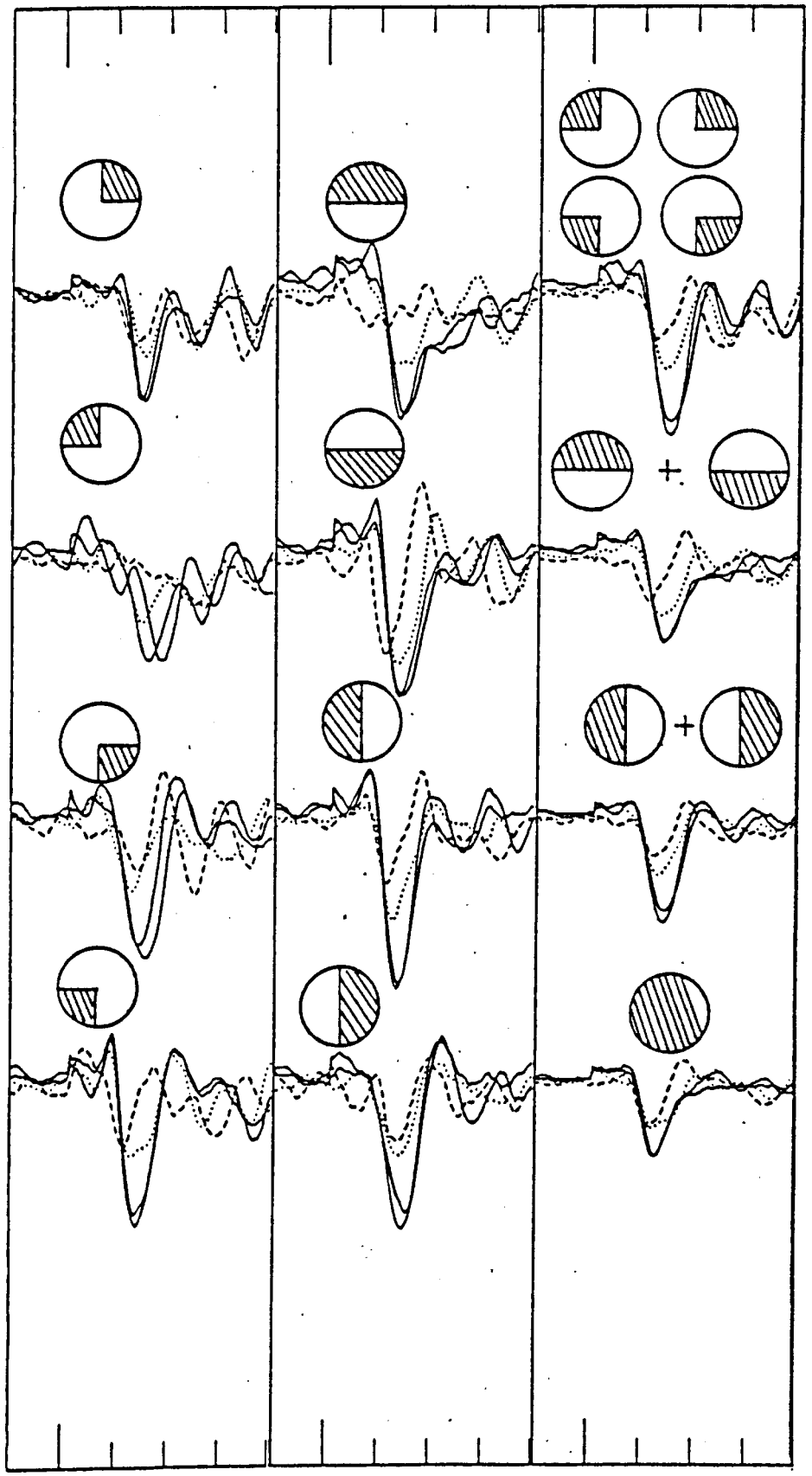
VEPs recorded from bipolar placement 7 in experiment 12.1.

Full traces for each pattern location are for isoluminant colour contrast and colour contrast + 80% transmission N.D. filter. Dotted trace is for monochromatic luminance contrast. Dashed trace for achromatic luminance contrast.

In column 3 the gain has been reduced by a factor of two for clarity of presentation.

Notice that at this electrode site the colour contrast VEP is always of larger amplitude than either of the maximal luminance contrast conditions. Also that the latency of the VEP elicited by achromatic luminance contrast is always shorter than that the monochromatic luminance contrast VEP, which in turn is shorter than that of both the colour contrast VEPs.

These data suggest that colour contrast stimuli may stimulated an additional number of cortical cells.



stimulation.

The major difference between colour and luminance contrast VEPs appears to be one of latency; isoluminant colour contrast VEPs tend to be longer by some 10-15 msec, this being the case for both of the major pattern specific components. These results imply that the areas of visual cortex generating contrast VEPs do so irrespective of the form of the contrast, which suggest in turn that the underlying neural population is equally sensitive to discontinuities of wavelength and of luminance, as indeed the work of Gouras & Kruger (1979) and Thorell et al (1979) would suggest.

An explanation of the increased VEP latency for isoluminant contrast stimuli has been offered in chapter 11.

The absence of any VEP component specific to colour contrast does not of course imply that the the human visual cortex lacks a functional area specifically processing wavelength differences. It may after all be the case that, for the subjects studied, this component cannot be identified because the underlying generator lies buried within the cortex, or indeed the optimal stimulus conditions for activating this region may not have been used. Alternatively, the prediction that there should be a 'colour specific' component may be misplaced. The only major and consistent difference between conditions in this study was that found for the negative potential, observed in the longitudinal mapping for both subjects. This peak was consistently larger for colour contrast patterns which suggest that under these conditions some other activity is contributing to the recorded response, although this is not readily apparent in the monopolar electrodes. Further studies will be needed to determine whether this is in fact the case. The limited evidence presented here suggest that the amplitude of this peak varies as a function of retinal location, and is approximately twice the amplitude of the comparable latency activity observed with luminance contrast stimulation. However for the latter, peak amplitude is again larger for monochromatic as compared to achromatic luminance stimulation (compare for example the responses shown in figure 12.16).

It is conceivable therefore, that some cortical site other than those which generate the later components of the onset VEP, is activated by chromatic stimuli. More extensive studies on a larger population of subjects will be needed to determine whether this is indeed the case.

Chapter 13:- Properties of CI component

Introduction

Jeffreys (1977) has shown that the CII component is almost entirely contour specific (see chapter 1 for definition). Whilst it is known that visual contours are the most significant feature of a stimulus, carrying more information than areas lying within them, it is difficult to relate the specific properties displayed by CII to any particular psychophysical phenomena. Similarly, single unit correlates of the 'outlining' effect have not been reported. The neural mechanisms which presumably mediate the contour specificity of CII are likely to be complex. Yet the existence of the effect is compelling evidence not only of the potency of visual contour, but for the existence within human visual cortex of specific mechanisms processing them. CI however appears only partially contour specific, and Jeffreys (1977) has suggested that this component may be composed of two sub-components, which he has called 'contour' specific and 'contrast' specific.

A further difference between CI and CII is their relative monocular/binocular ratios. The amplitude of CII, is for example, the same whether the stimulus is viewed with one eye or two. This finding is entirely consistent with the notion that within the extrastriate regions, cortical cells are primarily binocularly driven as suggested by the data of Zeki (1978) for areas V2 & V3 in monkey (see figure 1.4, chapter 1).

CI however has a different binocular/monocular ratio, and on the basis of adaptation studies, Smith & Jeffreys (1979) suggested that approximately 50% of striate cells are monocularly driven. It is not known however whether the contour and contrast specific activities within CI have a similar binocular/monocular ratio.

The properties of VEP components may reveal types of processing not evident at the single unit level. The experiments in this chapter will attempt to characterise these properties.

Experiment 13.1 :- Properties of contrast and contour specific CI

This experiment was conducted to examine the properties of the

contrast and contour specific components of CI. Because it has been shown that the 'outlining' effect produced by high contrast stimuli, and distinct from that studied by Spekreijse et al (1973), is limited to patterns with discrete elements a range of isolated square patterns of varying in square size, were used. The inter-element spacing in each case was equal to the square size. These stimuli were presented into either a blank field of the same overall mean luminance or into a field containing a pattern of thin outlines which marked the major contrast borders. The width of the outlines was 0.1mm (0.6'arc) and these patterns were exactly aligned with the contours of the contrast squares (see figure 1.3 in chapter 1).

The stimulus duration was 200 and 150 msec. Two subjects were used.

1mm = 6'arc.

For each condition 5 or 7 runs of 10 averages were undertaken.

Results

In figure 13.1 are shown for the two subjects the VEPs elicited by contrast squares and outline squares of varying size. It is evident that the peak latency of the VEP for contrast squares (dashed waveform) is shorter than that for the same sized outline squares across the whole range.

However, the latency difference is not constant as it appears that the peak latency of VEPs evoked by contrast squares is dependent on square size. The increase being approximately 25 msec across the range for squares of between 9'arc and 1.5 degree of visual angle.

The VEPs elicited by outline squares have different properties, the latency of the peak elicited by them is in fact independent of square size. This is clearly shown in figure 13.2 where the all VEPs for the two conditions have been superimposed.

Figure 13.3 shows the VEPs elicited by the presentation of contrast squares into the outline squares. Also shown are the VEPs obtained to the contrast squares presented into the blank field. Two features are evident. Firstly, the effect of the outlining on the VEP elicited by the contrast squares is to produce potential attenuation, even for large squares close to a 1 degree in side length. The extent of this attenuation can be gauged from a comparison of the hatched area.

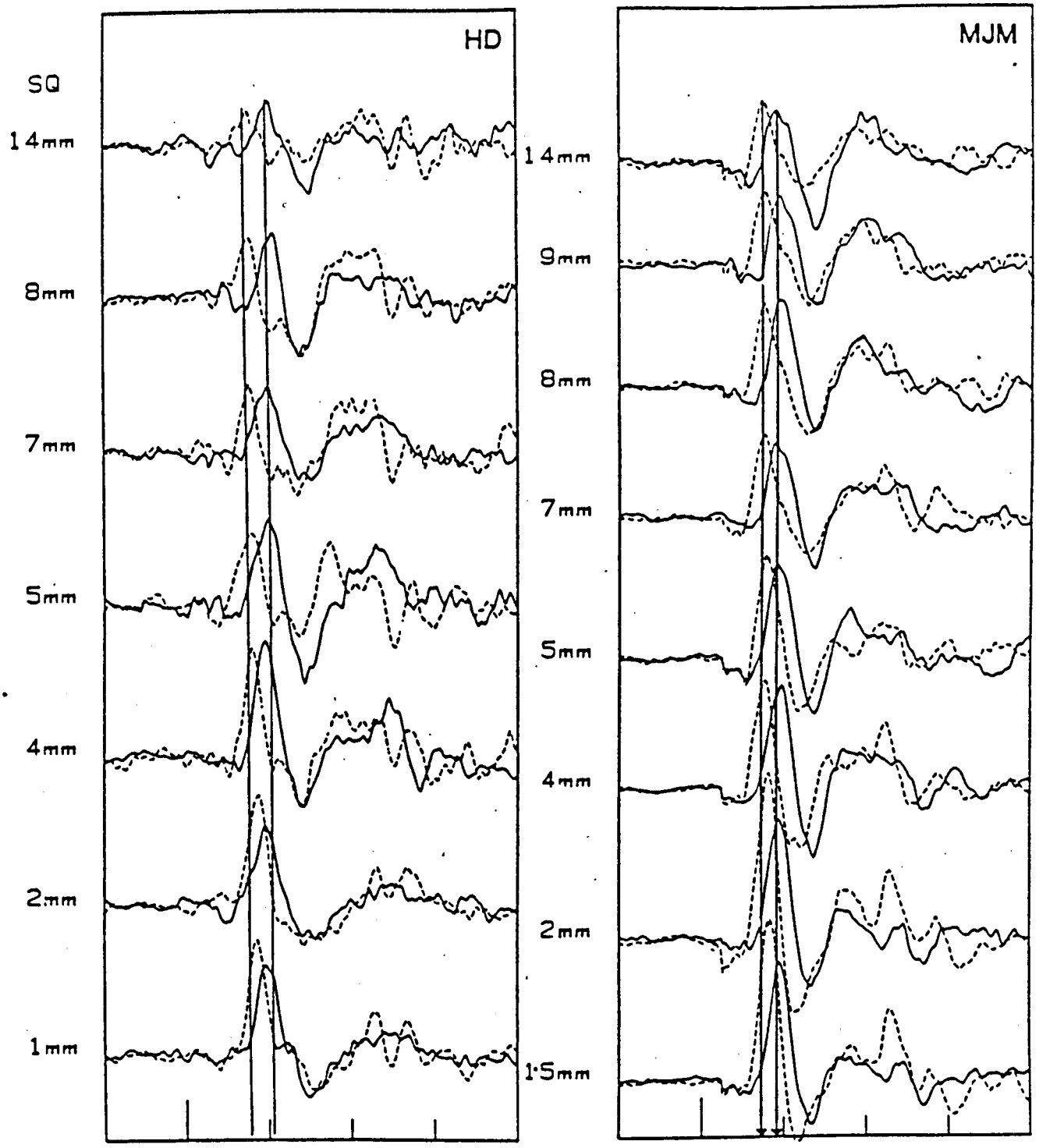


Figure 13.1

VEPs for two subjects elicted by contrast squares (dashed waveform) and outline squares (continuous waveform) of varying dimension.

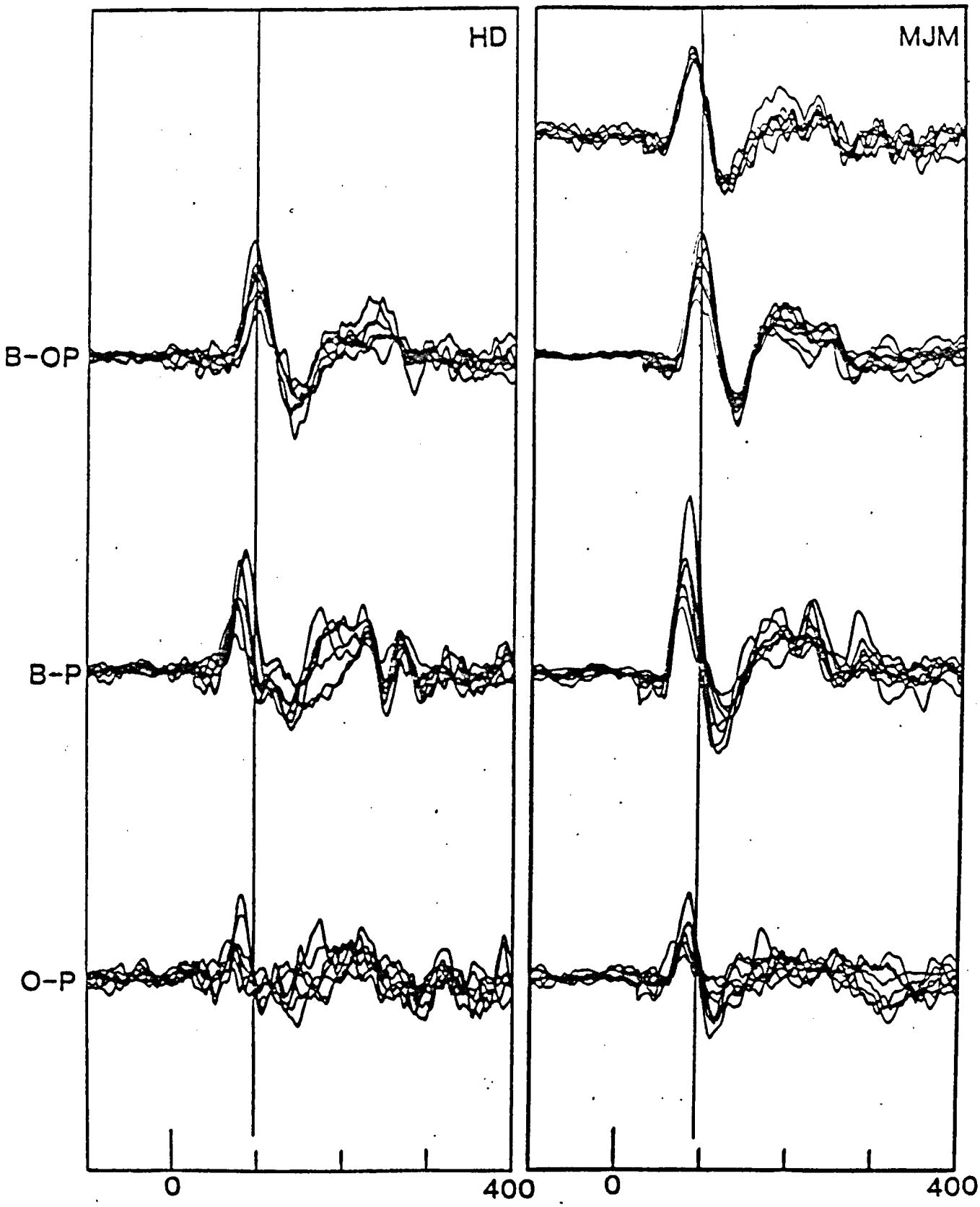


Figure 13.2

Superimposed VEPs for two subjects. B-OP = Blank to outline pattern. B-P = Blank to contrast square pattern. O-P = Outline to contrast square pattern. See text for discussion. The repeatabiltiy of these response are illustrated by the waveforms shown at top of left hand column for subject M.J.M. were the VEPs elicited by seven runs each of 8 presentations of the 2mm (12'arc) contrast square pattern have been superimposed.

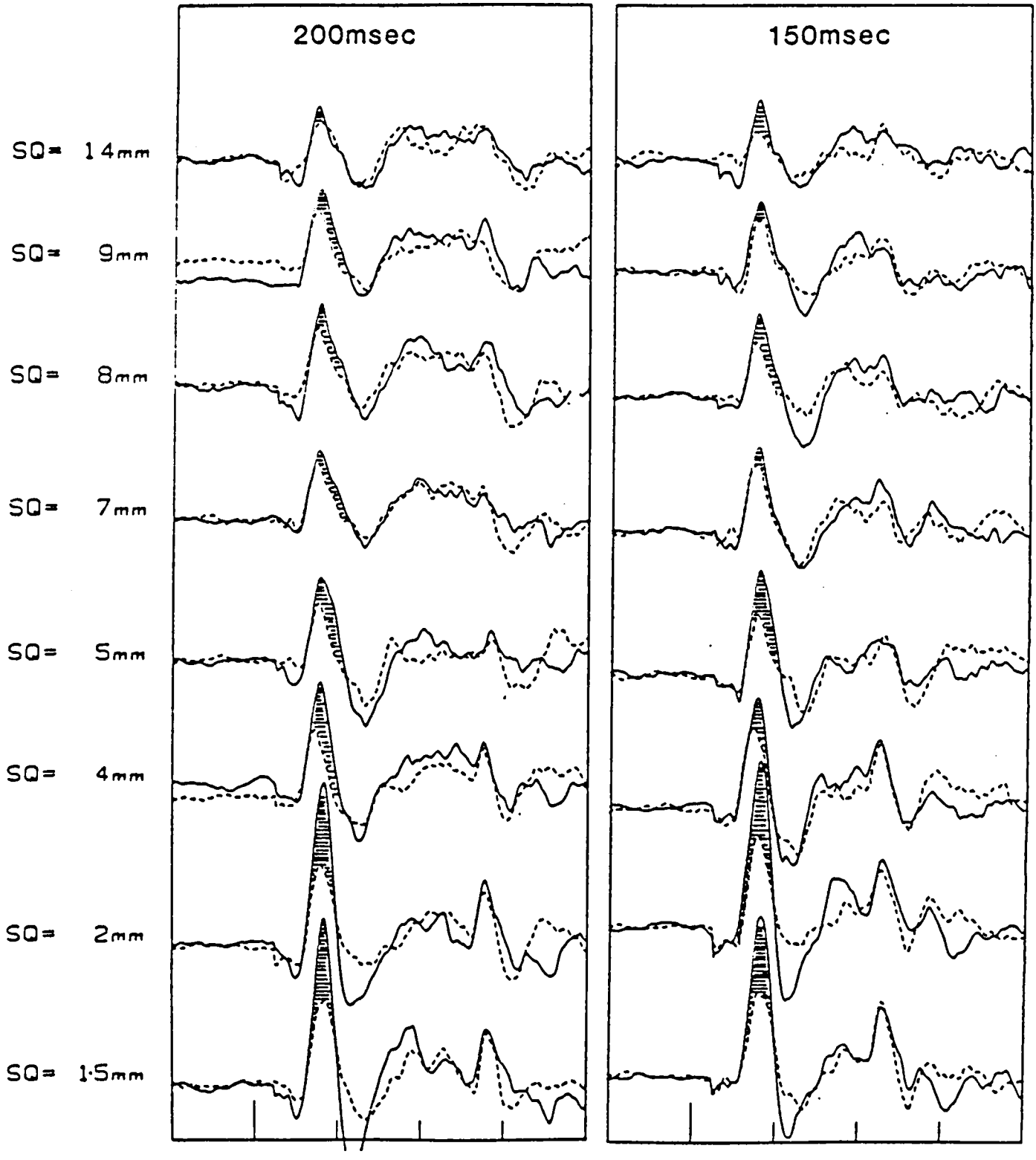


Figure 13.3

VEPs elicited by contrast squares (continuous trace) or by the presentation of these contrast squares into the thin outline square pattern. Stimulus duration 150 and 200 msec.

The second major feature is that the latency to peak of the outline-to-pattern VEP (from here on termed the contrast specific CI) is in fact shorter than that of the VEP produced by presenting the same pattern into a blank field. The extent of this latency increase is, (see figure 13.3), dependent on square size, up to a certain value, beyond which there appears to be little difference in peak latency between the contrast specific CI and that of the blank-to-pattern CI. This effect has also been observed by D.A.Jeffreys (unpublished experiments).

In figure 13.4 are shown the contrast and contour specific portion of CI, the latter obtained by subtracting the outline-to-pattern VEP from that to the blank-to-pattern VEP. Two features are evident. Firstly, the contour specific activity makes a progressively greater contribution to the blank-to-pattern VEPs as stimulus size is reduced, contributing less to the VEPs elicited by the patterns of larger squares.

The second feature which is perhaps most significant is that whereas the latency of the contrast specific portion of CI appears to depend on element size, the latency of the contour specific component appears to be independent of element size remaining approximately constant over the range used. Whilst the actual latency of the contour specific portion is shorter than that of the VEP elicited by the appearance of the outline pattern, the fact that under both conditions the latency to peak of the VEP is in fact independent of element size suggest that in each case that similar mechanisms are being stimulated.

13.2:- Discussion

The results of these experiments have revealed a number of interesting properties of the CI component, which suggest the existence of two distinct processing mechanisms within the striate cortex. These properties are difficult to relate to those of single units.

The shorter response latency of the 'contrast' specific component obviously reflects the activity of processes whose onset-latency is a decreasing function of contrast area. There must be a

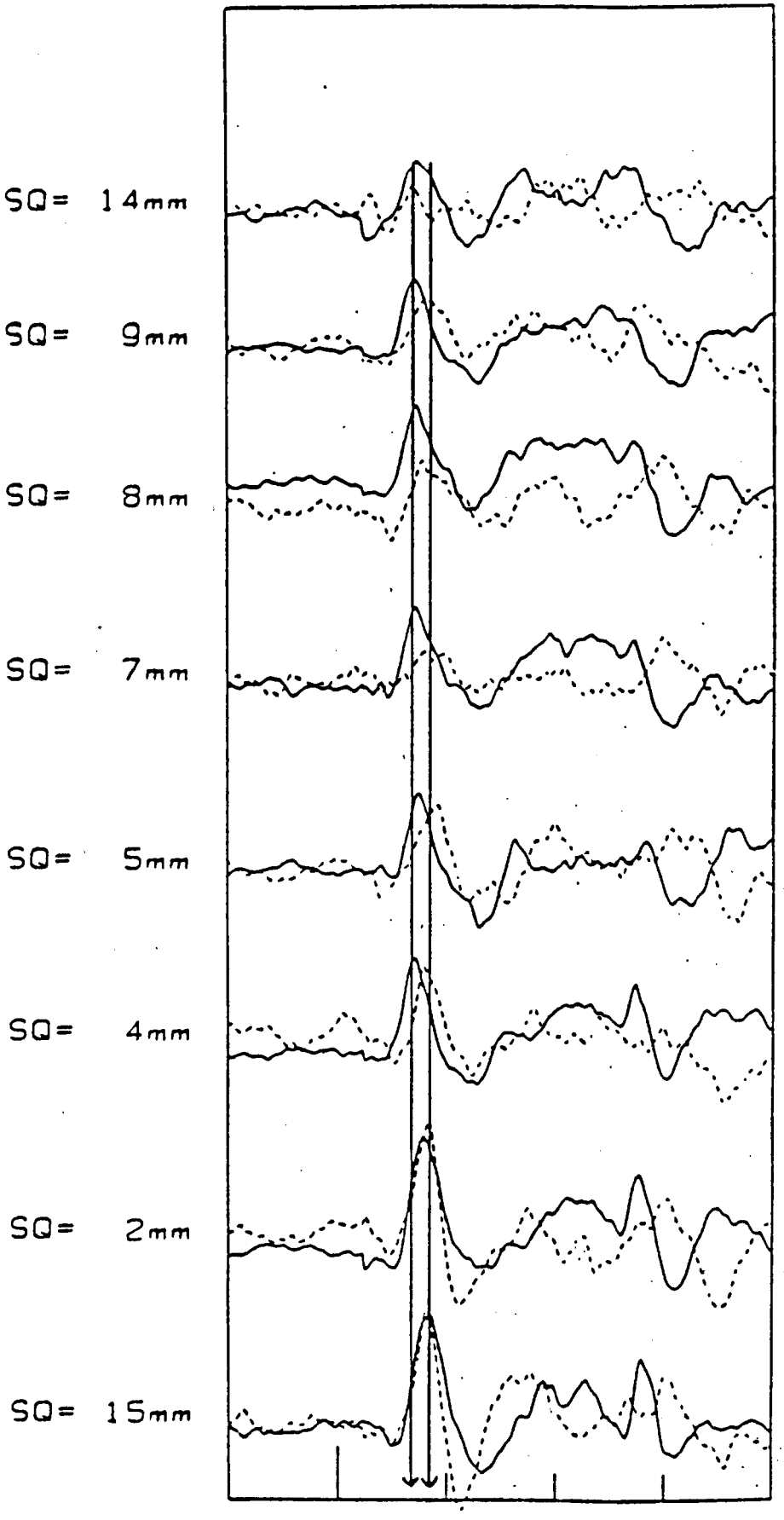


Figure 13.4

VEPs elicited by contrast squares presented into outline squares (continuous trace). Dashed waveform is obtained by subtracting this waveform from that produced by presenting the contrast squares into the blank field. See text for discussion.

limiting factor to this latency decrease because as contrast area increases the stimulus will begin to take the form of an overall change of luminance, under these conditions, the CI component cannot be recorded. The 'contrast' specific component seems to reflect activity at the initial stage of processing within striate cortex. Evidence consistent with this suggestion comes from Mitzdorf & Singer's (1978) studies which indicate that electrical stimulation of monkey optic chiasm or optic radiation produces excitatory synaptic activity within laminae of striate cortex that are divisable into two latency ranges. The initial phase is observed within layer IV and reflects monosynaptic activity, whilst the second phase is relayed from the monosynaptic responses, over two synaptic steps, to both superficial and deep layer cells. The present VEP data might be explained in the following way.

The contour-specific component however might be expected to reflect superficial layer activity. A number of features support this suggestion, the first of which is obviously its relative increased latency, which implies some latter stage of processing within the same anatomical region. Secondly, the properties of the component must, by definition, be determined by more complex types of neural processing, and it is known that in the superficial layers of monkey striate cortex a high percentage of 'complex' type cells predominate (Judge et al,1980; Hubel & Wiesel,1977). Moreover it is known that the superficial layers project mainly to visual area 18 and if, as noted previously, the CII component reflects activity from this area then the similarities between the properties of the contour specific CI and the properties of CII would perhaps be expected; CII reflecting a refinement of processing initiated by the superficial layers of V1. As shown below the similarity between the binocular/monocular ratio of CII and contour specific CI further supports the prediction that the latter reflects a later stage of processing within the striate cortex.

However Jeffreys (personal communication) has suggested that the latency difference between the contour and contrast specific components of CI may reflect a latency difference between two separate inputs to the striate cortex. Whilst there is indeed evidence for this in monkey (see section 1.5 of chapter 1), the latency difference reported are smaller than those observed here; although of course the studies are not directly comparable. Jeffreys has reasoned that if the latency differences were due to intracortical processing then they should be independent of square size, but as shown in figure 13.3 they are not, thus supporting Jeffreys suggestion. However if the latency difference

were due to differential conduction velocity or onset latency of two independent sub-cortical pathways then it would be predicted that the latency of the start of the deflection should be a decreasing function of square size. As evident from the VEPs recorded in the outline-to-pattern condition there is no apparent increase in onset latency with decreasing square size.

13.3:- Binocular/monocular ratio of 'contour' and 'contrast' specific CI.

As previously noted Jeffreys (1977) has suggested that the binocular/monocular ratio of CII is approximately 1. Smith & Jeffreys (1979) have shown that the degree of interocular transfer of CII is almost complete, whereas that of CI is only is only 50%. Their suggestion, which would be consistent with the single unit data, was that there are differences in the percentages of monocularly driven cells within striate and extrastriate cortex. In the following experiments, the binocular/monocular ratio of the contrast and contour specific components of CI will be examined.

Results

In figure 13.5, the amplitude of CI elicited with blank-to-pattern or outline-to-pattern stimulation are plotted as bar histograms, for both monocular and binocular stimulation. Also plotted is the residual VEP amplitude which remains when the outline-to-pattern VEP is subtracted from the blank-to-pattern VEP. This in effect is a measure of the extent to which outlining attenuates the overall response. The binocular monocular ratio of the VEP elicited by blank-to-pattern stimulation was $\sqrt{1.44}$ (2mm squares) and $\sqrt{1.6}$ (4mm squares) for subject M.J.M. and $\sqrt{1.47}$ (2mm squares) and $\sqrt{1.6}$ (4mm squares) for subject H.D. The ratios for the contrast specific component were $\sqrt{2.16}$ (2mm) and $\sqrt{1.99}$ (4mm) for subject M.J.M. and $\sqrt{2.0}$ (2mm) and $\sqrt{2.0}$ (4mm) for H.D. For the contour specific component the ratios were $\sqrt{1.0}$ (2mm) and $\sqrt{1.08}$ (4mm) for M.J.M and $\sqrt{1.09}$ (2mm) and $\sqrt{1.1}$ (4mm) for subject H.D.

Figure 13.5

Plots of VEP amplitude for the three conditions used in this experiment.

A= Outline to pattern condition

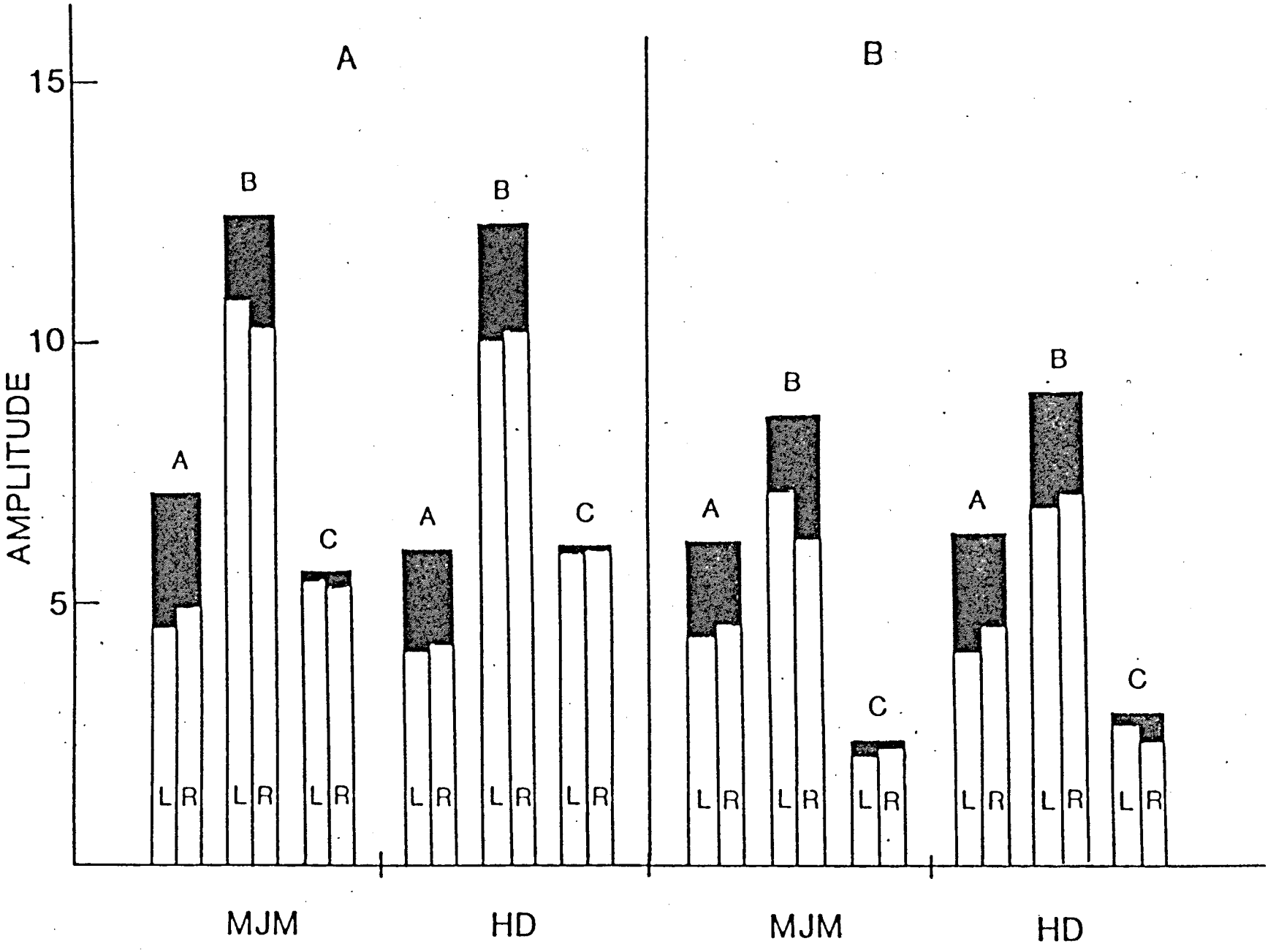
B= Blank to pattern condition

C= Blank to pattern VEP - outline to pattern VEP.

L= Left eye.

R= Right eye.

Plots on the left of the figure are for a 2mm (12'arc) isolated square pattern, plots of right for a 4mm (24'arc) isolated square pattern.


A
B
15
10
5
AMPLITUDE
A
B
C
A
B
C
L R
MJM
HD
MJM
HD

Discussion

These results have shown that that contrast and contour specific components of CI have different binocular/monocular ratios. This finding suggest that these components reflect the activity of two differing types of neural activity within striate cortex. If, as suggested above the contrast specific component, with its shorter response latency reflects an initial stage of processing within striate cortex then one would predict, on the basis of single unit data, that this activity is mediated by cells having a primarily monocular drive.

The contour specific component which has a binocular/monocular ratio similar to that reported by Jeffreys (1977) for CII, would appear to have properties consistent with it reflecting activity of neural mechanisms receiving a mainly binocular input. This would be consistent with the notion that contour specific CI reflects a later stage of processing, as suggested by a comparison of its latency with that of the contrast specific CI.

13.4:- Orientation Anisotropy of CI

A number of psychophysical studies have reported differences in contrast sensitivity as a function of grating orientation (e.g.Appelle,1972). These results have been interpreted as reflecting the higher preponderance of cells tuned to the vertical and horizontal, and support for this conclusion has been obtained from single unit studies of monkey striate cortex, where it has been shown that, over a random sample, the percentage of cells with vertically and horizontally orientated receptive fields is higher than those maximally sensitive to oblique orientations (Mansfield,1974 Mansfield & Rosner,1978).

Smith (1978) (unpublished doctoral thesis) has attempted to find electrophysiological evidence of meridional differences in sensitivity by comparing the properties of CI to briefly presented gratings of various orientation. His results did not support those of Maffei & Campbell (1970) who reported that, for the steady state VEPs meridional amplitude variations can be observed for gratings of intermediate to high spatial frequency. The differences between the results of these studies were explained by Smith in terms of differences in the stimulus pattern. Smith had used square wave gratings of 2 cpd as opposed to the 10 cpd sine waves used by Maffei & Campbell (1970).

It was noted by Smith that the major contribution to CI comes from the para and peri-foveal regions of the visual field. Single unit studies have reported that meridional differences in cell populations occur only in the central 5 degrees of the visual field. Thus the absence of meridional sensitivity of CI may reflect the major non-foveal contribution to this component.

Neither of these explanations are however adequate to explain the reported differences. Firstly, the CI component can be elicited by gratings of medium to high spatial frequency (see chapter 7).

Secondly, CI does contain a foveal contribution, although a 2 cpd grating would of course be an unsuitable stimulus for recording it because of the small number of contrast borders.

In the following experiments, the meridional sensitivity of foveal CI is examined.

Procedure and Methods

A positive contrast square wave grating of 12 cpd was masked to subtend a visual angle of 1 degree, and presented to the central left half-field. The luminance of the blank field, of 9x9 degrees, was 300

cdm^{-2} and the illuminance of the grating bars adjusted so that the pattern had a duration threshold of 2 msec.

The grating was presented at four orientations 0 dgrees (vertical), 90 degrees (horizontal), 45 and 135 degrees.

As a result of the decreased effectiveness of the pattern in evoking VEPs under these conditions 7 runs of 8 sweeps were undertaken for each condition. As Smith (1979) has suggested meridional sensitivities might be reflected in either the amplitude of the potential at saturation (as indeed Maffei & Campbells data would imply), or, more probably, in differences at sub-saturation levels. Therefore amplitude was measured as a function of subjective contrast over a range from threshold to suprathreshold levels. Two subjects with large and easily identified CI components were studied.

Results

In figure 13.7 are shown the superimposed waveforms for each series, each waveform representing the average of 42 sweeps, whilst in figure 13.9 the amplitude of the VEP is plotted as a function both of stimulus duration at each orientation and of the mean amplitude of the VEP to the vertical & horizontal, or oblique gratings, again as a function of stimulus duration. The slope of these amplitude function indicate a increase for both oblique and horizontal or vertical gratings. Measurements of peak latency also indicated no difference between conditions.

The data suggest therefore that there are no meridional variations in the percentage of the cell population within the striate cortex of man at least within the foveal representation of that region for stimuli of variable subjective contrast.

Discussion

The results of this experiment are at variance with the data of Mansfield (1974), but consistent with the findings of Finlay, Schiller & Volman both of whom recorded from monkey striate cortex.

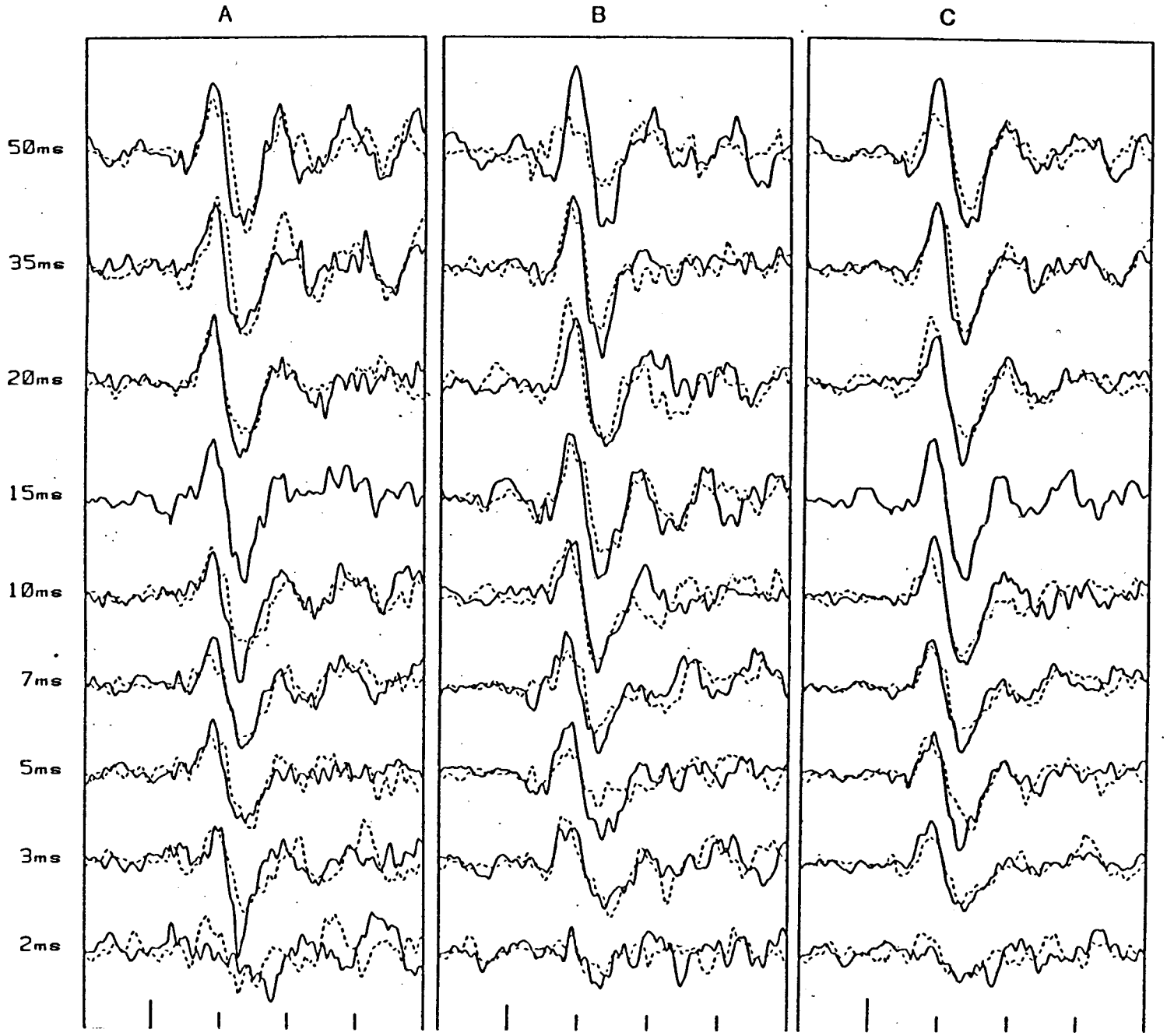
Recently, Blakemore (1981), in a detailed study of over 1000 cells within striate cortex of monkey, has reported evidence of small, but statistically significant, meridional differences in cell populations which he considered was consistent with the findings of Mansfield & Rosner (1978). However a number of points need to be made both with regard to this specific experiment and to single unit correlates of meridional acuity.

Figure 13.7

Column A:- waveforms in continuous trace are for vertical grating those in the dashed trace for a grating at 45' to vertical.

Column B:- waveforms in continuous trace are for horizontal grating dashed trace for a grating at 135' to vertical.

Column C:- waveform in continuous trace are the sum of the VEPs elicited by the horizontal and vertical gratings those in dashed trace the sum of the VEPs elicited by the grating at 45' and 135' to the vertical. Stimulus duration are shown at the side of column A.


A
B
C
50ms
35ms
20ms
15ms
10ms
7ms
5ms
3ms
2ms

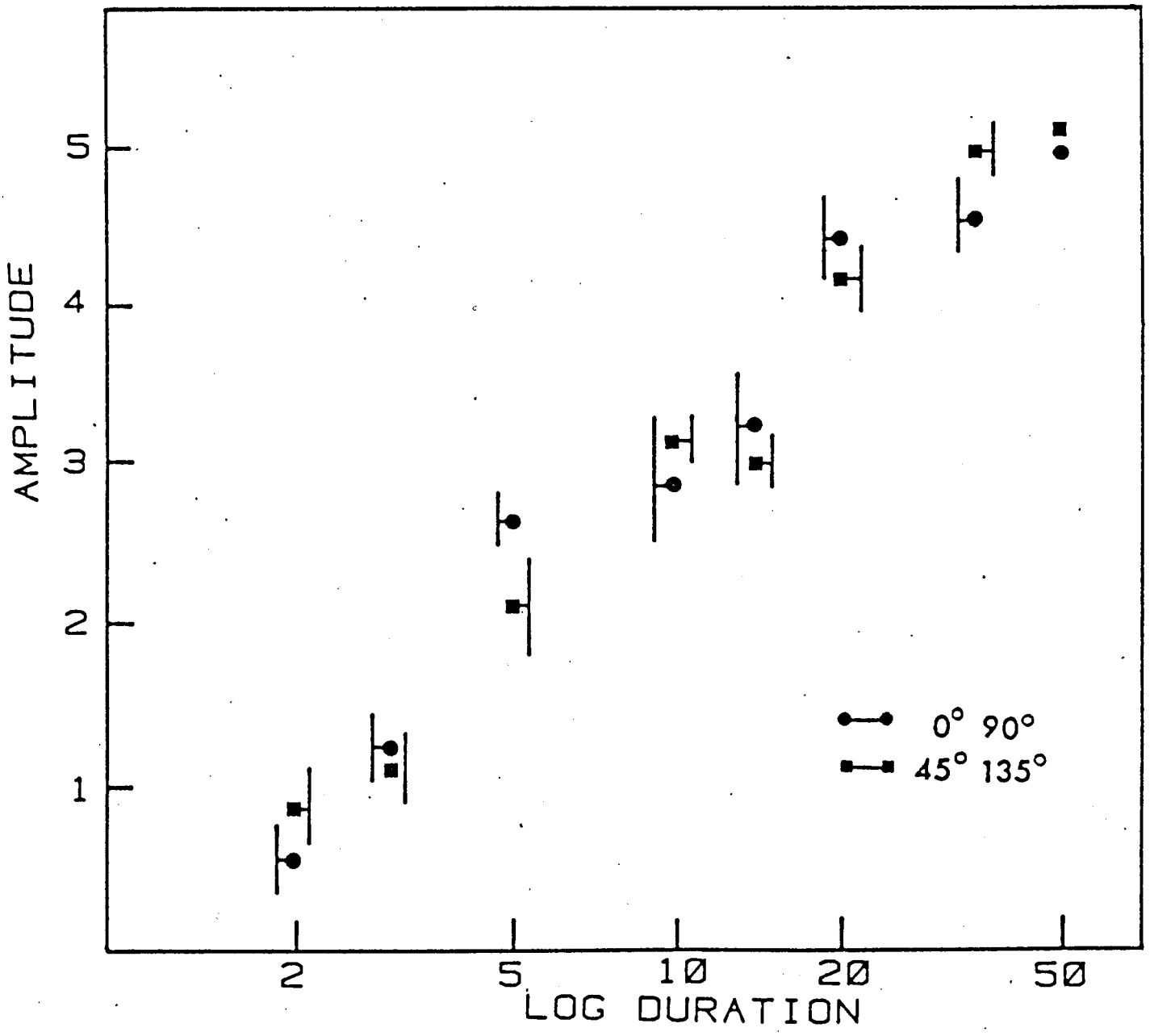


Figure 13.8

Mean amplitude of CI as a function of stimulus duration. Data for oblique orientations has been pooled as has the vertical and horizontal conditions.

Firstly, despite the large number of cells sampled in Blakemore's study they were not all for the same animal, in fact they reflect the selective sampling of cells from over 25 monkeys. Moreover because his stimuli were hand held, vertical and horizontal movements by the experimentor are more probable than oblique ones, and so it is possible that a sampling bias was introduced (no statistical analysis was for example given of the probability of a particular direction of stimulus movement on any one trial).

Secondly, those studies which have reported differences, show significant variations in the extent of meridional sensitivity. For example, Williams et al (1981) in a study of four macaque monkey reported that whilst all monkeys showed some orientation specific variations in contrast sensitivity for grating stimuli, the actual variations differed markedly, even in this small and genetically homogeneous population. Similar individual and group variations have been reported for human subjects (Zemon et al, 1980; Mitchell et al, 1967). It would appear that, whatever the underlying cause of meridional variations of contrast sensitivity, they are unlikely to be explained by a differential proportion of cells which are optimally sensitive to the vertical and horizontal.

13.5:- Effects of retinal illuminance on properties of CI component

It is well known that retinal illuminance has a marked effect on the dynamic properties of the visual system since it determines whether vision will be mediated by the photopic or scotopic system, which are thought to have different dynamic properties (see for example Foster,1978).

Illuminance has been shown to influence the response of retinal ganglion cells in the cat, a decrease causing a progressive increase in response latency and reduction in discharge intensity. (Levick & Zacks,1970; Gouras & Link,1968). Illuminance also effects the properties of cortical mechanisms. Halliday (1977) has shown that the latency of the pattern-reversal VEP increases as luminance decreases and has also reported that the amplitude of the response is progressively reduced. However, Van der Tweel et al (1979) have shown that, whilst a progressive decrease in retinal illuminance increases VEP latency, its amplitude can be shown to remain approximately constant if at each level of illuminance the contrast of the pattern is a fixed multiple of the psychophysically determined contrast threshold. This finding suggests a distinction between the factors which determine the latency and intensity of cortical activity, a distinction which appears evident in the post-stimulus time histograms of retinal ganglion cell activity as shown by figure 3. chapter 3.

If the generators of these VEP components are activated by the appearence of spatial contrast, then the amplitude of the VEP should be independent of retinal illuminance. This conclusion was drawn by Van der Tweel (1979). There is a further discrepancy between the data reported by Halliday (1977) and Van der Tweel (1979). The former had reported a 15 msec increase in latency per decade of illuminance, the latter a 30 msec increases per log unit. The discrepancy may be due to the fact that the Halliday had examined the reversal response, elicited by high contrast patterns, and no attempt was made to control for the effects of saturation. Van der Tweel et al (1979) had however used a checkerboard pattern with large check sizes (40-60'arc) and it is known that stimuli of this angular subtense elicit VEPs which are similar in form to the luminance VEP.

The present study will examine the effects of adaptation level on the properties of the CI component elicited by isolated square patterns.

Procedure and Methods

Stimuli of positive contrast were presented into the left half of a 5 degree field. Retinal illuminance was varied by inserting neutral density filters of 1 log unit value. The isolated squares squares had a side length of 18'arc.

In Van der Tweel's study stimuli were presented at a fixed multiple of the psychophysically determined contrast threshold at each adaptation level, however Tachistoscope A does not allow the easy determination of contrast thresholds and to overcome this limitation the following method was employed. At each adaptation level, stimulus duration was reduced to 5 msec, and the illuminance of the positive contrast elements reduced until the pattern was just at threshold; VEPs were then recorded for stimuli presented at twice and four times this duration.

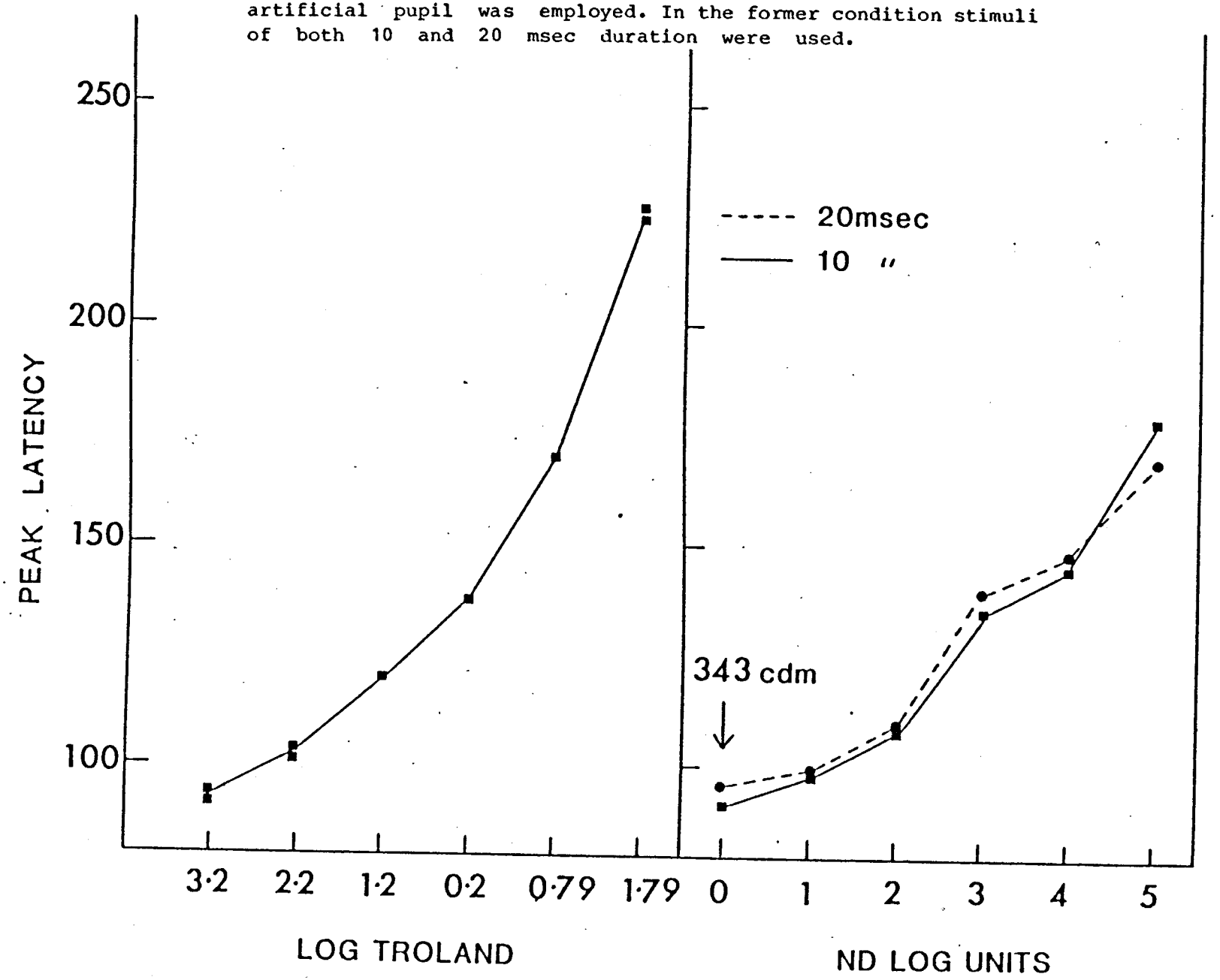
Both natural and artificial pupils (3.5mm), were used and viewing was binocular.

Results

The principal results of these experiments can be simply stated: a reducing retinal illuminance from medium photopic to scotopic levels produces a progressive increase in component peak latency. This is illustrated in figure 13.9 where peak latency has been plotted as a function of retinal illuminance, expressed in log trolands values, for the case where an artificial pupil was used, and as a function of log field illuminance where natural viewing was used. The latency increase is approximately linear over a 5 log troland range below 3.2 log trolands. The actual amount of this latency increase per log troland is approximately 24 msec, although there is some evidence of saturation at higher levels. The overall increase in latency observed under natural viewing is less than that observed with artificial pupils and amounts to 17-20 msec per log unit decrement, for both the 10 and 20 msec duration stimuli. The discrepancy observed here appears to be related to pupil size and hence retinal illuminance. The present values are intermediate between those reported by Halliday (1977) and Van der Tweel (1979), and the latency differences observed between VEPs recorded under natural and artificial pupils may account for the 15 msec per log unit difference of the above two studies. However, neither

Figure 13.9

Plots of peak latency as a function of background illuminance and retinal illuminance, for the case where an artificial pupil was employed. In the former condition stimuli of both 10 and 20 msec duration were used.



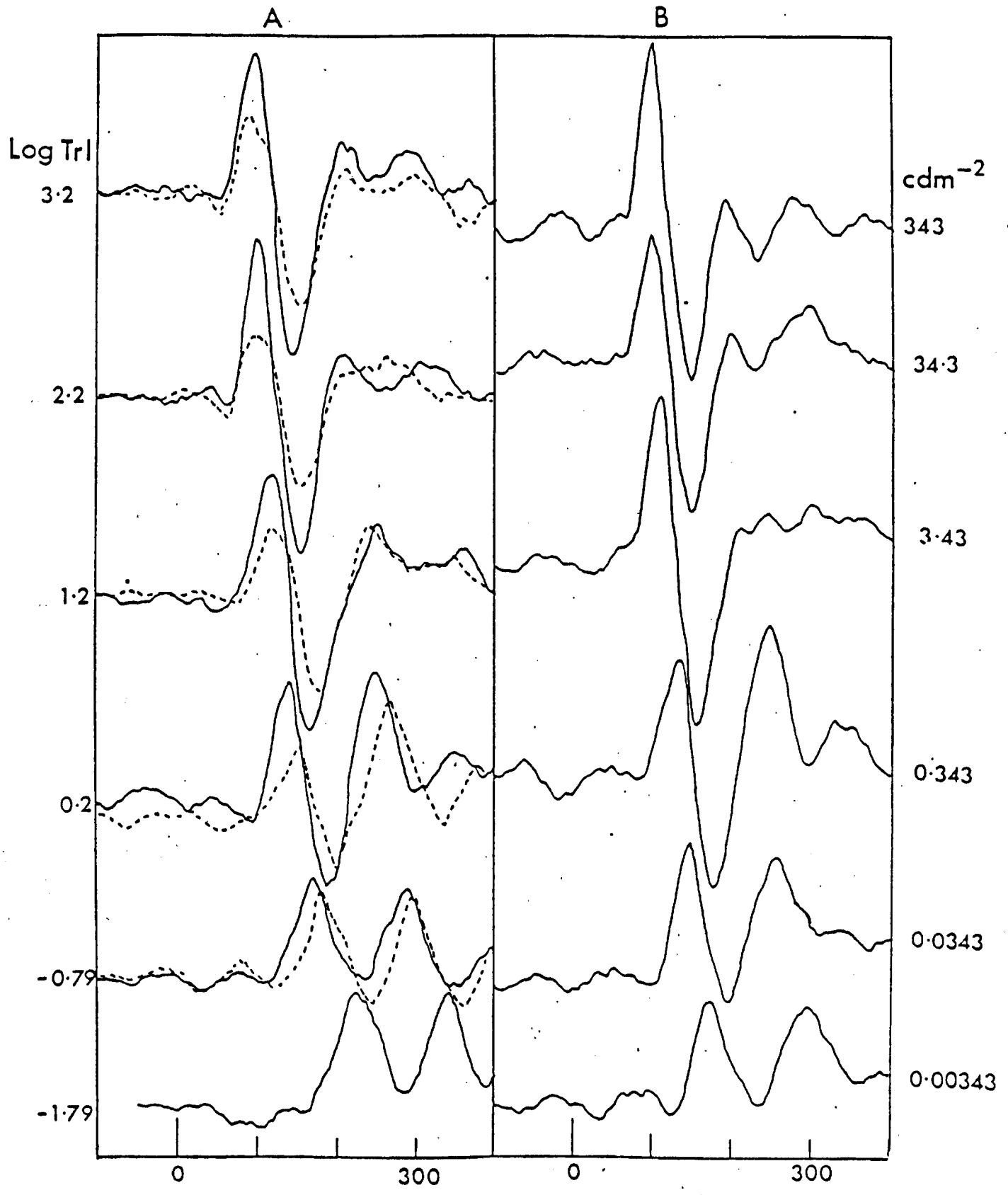


Figure 13.10

VEP elicited under conditions of decreasing retinal or background illuminance. In condition A the continuous waveform was elicited by a stimulus of 20 msec duration and the dashed trace by a stimulus of 10 msec. At each level threshold duration was set to be 5 msec. In conditions B stimulus duration was 20 msec.

of these studies reported the sampling rate (in the present case it was 1 msec), or decribe how latency values were determined and it is thus difficult to draw any firm conclusion from these discrepancies.

Van der Tweel (1979) had noted that there was little change in VEP waveshape and little decrease in amplitude even if retinal illuminance was in the scotopic range. This phenomenon is evident in figure 13.10 where despite a 5 log unit decrease in illuminance the amplitude of the VEP remains fairly constant under each of the two conditions.

As noted in chapter 3, Spekreijse et al (1973) had reported that at low levels of contrast or retinal illuminance VEP waveforms become more sluggish. There is some evidence that when the stimulus is viewed with an artificial pupil the VEP peak appears broader, particularly at levels of retinal illuminance below 0.2 log trolands. The amplitude remains fairly constant however, despite the pronounced differences in subjective brightness.

The results show that the effect of retinal illuminance on amplitude surprisingly small when pattern contrast is a fixed multiple of threshold contrast, a finding entirely consistent with the data of Van der Tweel, and which, in turn, implies that the dynamic characteristics of the mechanisms that generate the CI component are relatively independent of retinal illuminance.

The increase in latency observed here, amount to some 120 msec over a 5 log unit range a increase that is far in excess of that reported for CI under any other condition observed in this thesis. These are consistent however with the single unit data of Gouras (1965) who has examined the effects of illuminance on the latency of discharge of monkey retinal ganglion cells.

Chapter 14:- Conclusion

It has long been hoped that Visual Evoked Potentials could be used as a bridge by which to link psychophysical studies of the human with physiological studies of the mammalian visual systems. However a bridge can only be as good as the foundations upon which it is built. Many who have studied the VEP have done so with little consideration of the assumptions on which their study is based, and the data reported are often little more than descriptive (see for example Jones & Keck (1978) or Parker & Salzen (1977a,b)). As noted in the introduction to this thesis, the VEP in not a unitary phenomena and the approach taken in this study has been to examine specific properties of clearly identified VEP components under conditions in which they are efectively isolated from that of both preceding and succeeding activity.

The principal aim of this research has been to examine the properties of these components and then, where possible, to compare them with known single unit properties recorded under comparable conditions. Where similarities are observed comparable psychophysical functions are then compared, in an attempt to link the three approaches previously outlined.

The data presented in chapter 3 showed a close relationship between the properties of CI and those of single cells recorded in the cat. case. The time course of temporal integration of CI revealed a distinct dichotomy between those factors determining latency and amplitude functions, these being qualitively and quantitively consistent to that observed at the single unit level. These findings confirm that these VEP components are a meaningful reflection of underlying physiological activity within the human visual cortex.

The close relationship between the properties of CI and psychophysical and single unit functions was extended in chapters 4 and 5 by the finding that the time course of temporal summation of brief discrete pairs of patterned stimuli is quantitatively similar to that observed in psychophysical threshold studies, on the one hand, and with the time course of temporal summation shown by single units at retinal and geniculate level in the cat. The functions obtained are perhaps among the most conclusive evidence reported to link VEP, single unit and psychophysical data.

In chapter 6 an attempt was made to determine the relationship between steady state VEPs elicited by pattern-onset and the properties of CI. The results showed that the former have a similar retinal (pattern) position dependency, and scalp distribution to the latter and thus probably reflect activity within the same region of visual cortex. This was not the case however for steady state luminance onset VEPs. Further studies will be needed to determine, in more detail, the nature of this relationship. If, as the evidence seems overwhelmingly to suggest, that high frequency pattern-onset VEPs reflect activity within the same region of cortex as CI then those studies in which the steady state pattern VEP have been recorded without previously determining the distribution of transient pattern-onset activity (i.e., with a view to finding the ideal conditions for recording individual VEP components), will provide data of limited physiological significance. This finding may have significance for the interpretation of clinical VEPs which are used as an objective method of assessing the integrity of visual function.

Experiment 6.4 of chapter 6 confirmed Pieron's (1961) prediction that the dissociation between temporal resolution, as measured by CFF and double pulse resolution is the result of neural factors; specifically, the non-linearity of the system in response to discrete aperiodic aperiodic stimulation. Again, a close relationship between psychophysical and electrophysiological measurements was observed.

Thus the experiments conducted in the early chapters of this thesis have shown a close relationship between properties of CI and comparable single unit data. It appears therefore that CI is a meaningful indicator of contrast-dependent physiological activity within striate cortex. Having shown this to be the case the component was then studied under conditions, specifically designed to examine the predictions of some recent models of visual information processing which have suggested that the retino-cortical pathways are composed of two distinct processing channels, with differing spatial/temporal properties.

Whilst the data did not in any way support the predictions of these models, it did suggest that under some conditions the functions which are obtained are consistent with the operation of two distinct mechanisms. As discussed in chapter 13, these mechanisms may be related to the processing of 'contour' and 'contrast'. The respective VEP components reflecting this activity differ, not only their onset latencies, but also in their binocular/monocular ratio.

The psychophysical phenomenon of which the experiments in chapter 7 sought VEP correlates may reflect neuronal interactions at a stage of processing later than the striate cortex. This suggestion would be consistent with the single unit data monkey (Lee & Cleland,1980; Hicks et al,1981).

In chapter 8 and 9 the properties of CI and CII were examined under stimulus conditions which give rise to the phenomena of metacontrast and visual noise masking. The absence of target VEP attenuation observed under retroactive masking condition was again quantitatively consistent with comparable single unit data and proved conclusively that these psychophysical phenomena cannot be interpreted in terms of neural inhibition at, or prior to, the striate cortex. Indeed for retroactive noise masking the VEP functions compared almost precisely with those of single units recorded in the striate cortex of the macaque. However because VEPs reflect activity from a large number of neurons they provide a more comprehensive characterisation of the cortical response, particularly under the type of experimental conditions utilised in these chapters; moreover they have the added advantage that they can be directly compared to sensation. Thus the study of VEP component of predicted cortical origin can be studied to test the predictions of psychophysical models of visual information processing.

In chapter 11, the CI and CII components were shown to be sensitive to colour contrast stimulation. Unlike previous VEP studies (Regan,1972) it can be concluded from this data that many cells within human foveal striate and extrastriate cortex are sensitive to hue differences at isoluminance and must therefore receive input from two, or more, cone mechanisms. This conclusion is entirely consistent with the recently reported single unit data from comparable regions of the macaque visual cortex, implying that similar processing is undertaken in each (Gouras & Kruger,1979).

The temporal properties of these pattern-onset components under monochromatic luminance and colour contrast were similar to that reported psychophysically, which suggest that the poorer temporal discrimination observed in psychophysical studies of the socalled 'colour opponent' and 'luminance' channels (see Foster,1981) are determined by precortical factors.

The study of colour contrast VEPs was extended by the experiments of chapter 12 where a detailed examination of the scalp topography of VEPs elicited by chromatic, achromatic, and monochromatic luminance contrast was undertaken. Evidence was sought for colour specific VEP components, which might be predicted to occur on the basis of the single units data of Zeki (1978a) for the rhesus monkey. From the limited sample of subjects studied little evidence was found to suggest any VEP components specific to wavelength contrast. Similarly there was little evidence for any subtle change in scalp distribution of the major components of the pattern-onset VEP. Thus it appears that the sources of these components are as sensitive to colour contrast as they are to luminance contrast. However when VEPs were recorded from a particular electrode configeration potentials elicited by colour contrast were of significantly greater amplitude than those elicited by either monochromatic or achromatic luminance contrast, which suggest that 'colour contrast' stimuli activate a further population of cortical neurons. More detailed studies will be needed to determine the significance of this finding.

The research undertaken here has shown some close correlations between the porperties of VEP pattern-onset components and those of single units recorded from monkey visual cortex. These findings further support the model of Jeffreys & Axford (1972a,b), in this case by showing functional similarities between components and physiological activity in regions of cortex which are predicted, on the basis of their scalp topography, to be their source locus. Thus, by determining the anotomical and functional nature of these VEP components, it is possible to reveal hitherto unobtainable aspects of information processing within specific cortical sites. This may be particularly important for our future understanding of the relationship between physiology and perception. Obsession with the micro structure of cortical function, i.e., cellular receptive field properties, whilst interesting in its own right, detracts from the problems of relating information processing to more global physiological processes (see Chapter 9). A single cell, however interesting and specific its receptive field properties, is only one of a very large number which will be activated by complex visual stimuli, such as used in the experiments of this thesis. As Mackay (1980) has noted, the discharge of any one cell, viewed in isolation, would tell the system very little; information of lower statistical variance may be provided by "cooperative" activity between ensembles of cells, that may in turn be reflected in gross electrophysiological activity. (see also Pribram et al,1981)..

Future research, utilizing gross electrode and multi-unit techniques, (see for example Kruger & Bach,1980), combined with studies comparable to those of Jeffreys & Axford, would provide much needed insights into the overall relationship between these types of electrophysiological activity.

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