VISUAL MOTION-EVOKED POTENTIALS IN MAN

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Abstract

Visual motion-evoked potentials were recorded from the human scalp.

The stimulus chosen for most detailed study was sudden reversal of the motion of a patterned field, on the hypothesis that this was likely to activate only mechanisms selectively sensitive to the direction of stimulus motion. A large proportion of the experiments were designed to test this hypothesis; and in fact they supported it.

In addition to motion-reversal VEPs, VEPs to the onset and the offset of pattern motion, and to the appearance and disappearance of patterns were recorded and analysed. The relationships between these different types of VEP were investigated.

Also, the dependence of the motion-onset, -offset and -reversal VEPs on certain stimulus parameters was studied.

Are motion-reversal VEPs produced by direction-selective mechanisms?

That direction-selective mechanisms were at least partly responsible for the motion-reversal VEPs was confirmed, since an adapting stimulus moving in the same direction as the motion before reversal produced an effect on the VEP different to that produced by an adapting stimulus moving in the opposite direction.

Further investigation indicated that direction-selective mechanisms were probably the sole contributors to the motion-reversal VEPs, since control experiments failed to support any of the most likely alternative ways in which direction-insensitive mechanisms

might theoretically have contributed to the motion-reversal VEPs.

In particular, considerable attention was devoted to the possibility that mechanisms sensitive to contrast but insensitive to direction of motion might have been activated by a brief increase in the effective contrast of the stimulus pattern at the moment of reversal, and thereby have contributed to the VEP. Such an increase in the effective contrast could in theory have been caused by the brief slowing down which inevitably occurred at the moment of reversal, but several experiments refuted this interpretation. In particular, the VEPs were virtually independent of the time taken for reversal, but were very dependent on the velocity before and after reversal, reducing almost to zero at very high or very low velocities.

A sudden step-displacement or change of the pattern at the moment of reversal suppressed the VEP. This effect was not caused by interference with the time-course of slow movement at reversal, since suppression occurred even when the step-displacement took place outside the period of slow movement. A psychophysical effect has been observed which may be connected with this phenomenon.

Involuntary eye movements are apparently not implicated in the production of the VEPs, since periodic and aperiodic stimulation yield similar results.

Certain other ways in which VEP components might have arisen, even in the absence of eye movements or imperfections in the stimulus motion, have been investigated; but there has been no

indication of the occurrence of such components.

So the motion-reversal VEPs probably arose almost entirely from direction-selective mechanisms.

Component analysis of VEPs

The VEPs to the reversal and to the offset of motion apparently comprised three separate component peaks. In this respect they were similar to pattern-appearance VEPs, and the distribution over the scalp of any one of the components was the same for all three kinds of VEP (e.g. the first peak of the motion-reversal VEP had the same scalp-distribution as the first peak of the motion-offset VEP and the first peak of the pattern-appearance VEP). This implied that the corresponding components originated in the same cortical areas, and a correlation analysis of the amplitudes of the various components of motion-reversal VEPs and pattern-appearance VEPs for different subjects supported this conclusion. Now there is convincing evidence (Jeffreys, 1971) that the first component of pattern-appearance VEPs originates in striate cortex and the later components in extrastriate cortex. It is therefore concluded that the first peaks of motion-reversal and motion-offset VEPs are likewise probably from striate cortex, and the later peaks from extrastriate.

The VEP to motion-onset was very different from the above VEPs, however, and appeared to be more closely related to the pattern-disappearance VEP. It is possible that the same mechanisms underlie these two kinds of VEP.

Although motion-reversal VEPs appear to be the product of direction-selective mechanisms alone, it is far from certain that this is true of motion-onset and -offset VEPs. Nevertheless, there is evidence that the latter kinds of VEP may share generating mechanisms with the former; since the motion-reversal VEP was, under many conditions though not all, a good approximation to the sum of the motion-onset and -offset VEPs recorded under similar stimulus conditions.

The effects of varying stimulus parameters

Motion-reversal VEPs were found to be largely independent of brightness except at the lowest levels, but the latency did tend to increase slightly as the brightness was reduced.

Despite the discovery (MacKay & Rietveld, 1968) that the proximity of a stationary reference line enhances the VEP to the onset of motion of a stimulus line, it appears that the sharp contours comprising the edge of the visual field did not influence the VEPs to the onset, offset or reversal of pattern motion, since replacing the sharp contours by blurred ones did not affect the VEPs.

The onset, offset and reversal VEPs did not depend greatly on the direction of motion. Superimposing a steady motion did, however, markedly modify the VEPs.

The effects of using patterns other than visual noise were investigated. Checkerboards and visual noise produced similar results, but line rasters produced very different VEPs.

CHAPTER 1

Introduction

There are two main standpoints from which vision may be studied: psychophysics and electro-physiology. These two approaches are logically distinct, and complementary. Each is valid in its own right, but special interest attaches to the relationship between the two, that is, between the subjective experiences investigated in psychophysics and the objective recordings of electro-physiology. But herein lies a problem, for psychophysical investigations are almost always carried out on human subjects, whereas the bulk of visual physiology has to be done on lower animals, since surgery is usually involved. Partly for this reason, some researchers have been attracted to the technique of recording visual evoked potentials (VEPs) from the human scalp, as a "linking technique" (Campbell & Maffei, 1970). An additional advantage of VEPs is that they may show up features of large-scale activity in the nervous system that would not be detectable at the level of single units. Also, the larger scale of the data may facilitate comparison with psychophysical data.

In everyday experience of the visual world the presence of contours is much more important than the total amount of illumination, and cortical single neurones are likewise more sensitive to contours than to diffuse illumination (e.g. Hubel & Wiesel, 1962, 1965, 1968). This fact has prompted a number of investigators to study pattern-evoked potentials on the human scalp (e.g. Spehlmann, 1965; Spekreijse, 1966), and there is growing evidence that this line of research is

likely to be fruitful. (See subsection 1.1.2.).

Now motion is also a very important parameter for the stimulation of many cortical neurones (Hubel & Wiesel, 1962, 1965, 1968), which suggests that pattern motion may be an important stimulus parameter for VEPs; but there have so far been only a few brief publications dealing with this (Dawson, Perry & Childers, 1968; MacKay & Rietveld, 1968; Rietveld & MacKay, 1969a, b). Hence the choice of visual motion-evoked potentials as the subject for research to be outlined in this thesis.

1.1. Visual evoked potentials.

Visual stimulation with a bright flash produces a transient polyphasic potential change on the scalp, which is often detectable in the raw EEG. Early investigators of these "evoked potentials" relied on the radar technique of superimposition to enhance the signal-to-noise ratio ~~(Dawson, 1951)~~, but more recently averaging techniques have provided a better means of separating the evoked potentials from the background activity (Dawson, 1954; Clark, 1958; Goldstein, 1960; Halliday & Pitman, 1965). (And in this thesis all reference to VEPs must be understood to denote averaged evoked potentials.) If the noise is random, and independent of the signal, the signal-to-noise enhancement is equal to $\sqrt{n}$, where n is the number of averaging samples.

The VEPs recorded using the above averaging method can, of course, be produced only if the stimulus is repetitive at sharply defined moments of time at which the averaging apparatus can be triggered. Such VEPs are called "transient VEPs", and must be distinguished from

"steady-state VEPs", which are produced by modulating a stimulus parameter about a fixed level. The fundamental and higher harmonic components of the latter VEPs are extracted using cross-correlation techniques or by means of narrowly tuned band-pass filters. Steady-state VEPs will not be discussed further in this thesis, but they have been reviewed in MacKay (1969) and by Regan (1970).

In the following sub-sections, VEP research is reviewed, with special emphasis on pattern-evoked potentials and movement-evoked potentials, as these are the most relevant to the present thesis. (For more detailed reviews see MacKay, 1969; Perry & Childers, 1969; MacKay & Jeffreys, 1971; Regan, 1971.)

1.1.1. Flash-evoked potentials.

In the bulk of VEP research, flash has been the stimulus. It has been widely reported that the VEP to flash is very complex, polyphasic, and subject to considerable variation between individuals, but is consistent for repeated recordings from the same subject (e.g. Cobb, 1950; Monnier, 1952; Ciganek, 1961; Kooi & Bagchi, 1964).

The parameter which has been most studied in flash VEP research is luminance. At low luminances the VEP is biphasic, but as the luminance is increased, more components are added to the VEP which then becomes very complex (Tepas & Armington, 1962). The amplitudes of the early components, at any rate, increase systematically with luminance until saturation is reached; and the latency of all components decreases as luminance is increased (Tepas & Armington, 1962; Shipley et al., 1966).

Another important parameter is retinal area. According to DeVoe, Ripps & Vaughan (1968), flash VEPs are largely foveal in origin, but Eason et al. (1967) have reported responses due to flash stimulation of small areas more than 40° from the centre of vision. If small retinal areas are used, this helps to simplify the VEPs (Tepas & Armington, 1962), and some VEP components then exhibit polarity reversal between upper and lower half-fields (Schreinemachers & Henkes, 1968). The latter phenomenon is much more marked, however, with patterned stimulation, as will be seen in the next section.

1.1.2. Pattern-evoked potentials.

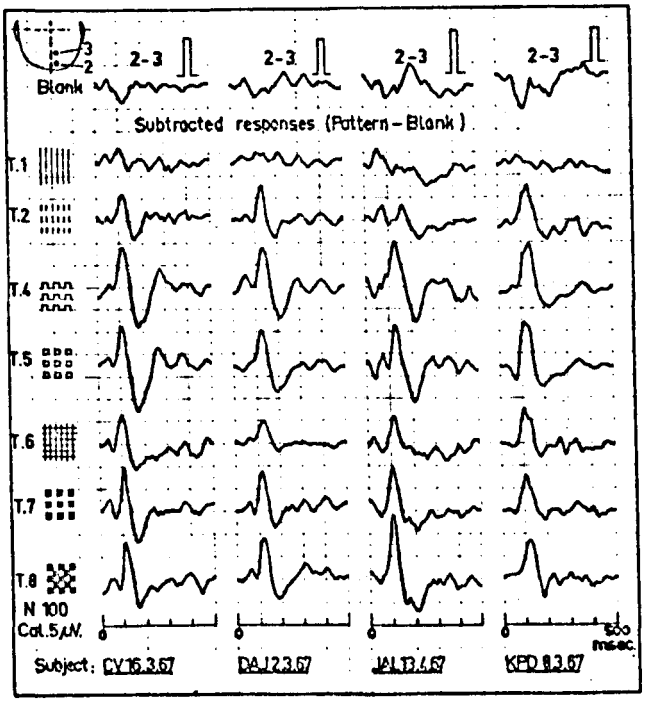
(a) Flashed pattern VEPs.

If the flash stimulus illuminates a patterned field instead of a homogeneous field, striking differences in the form of the VEPs result (Spehlmann, 1963, 1965; Chapman, 1965; John et al., 1967; Harter & White, 1968). The most pronounced changes are reported to be the reduction or reversal of polarity of a prominent 100 msec positive peak and the enhancement of a later (200 msec) positive peak. These VEPs to flashed pattern are sensitive to the parameters of the pattern. Flashed checkerboard VEPs were usually largest for check sizes in the range 10-20' (Spehlmann, 1965; Rietveld et al., 1967; Harter & White, 1968, 1970), but the optimal check size depended on the retinal area stimulated (Eason, White & Bartlett, 1970; Harter, 1970). Reducing the contour sharpness greatly diminished the pattern-related components (Spehlmann, 1965; Lifshitz, 1966; Clynes & Kohn, 1967) especially for the smaller (20') check sizes (Harter & White, 1968, 1970).

The effects of varying pattern luminance have been studied less, but it appears that the amplitudes of the main pattern-related components tend to increase with brightness while the latency decreases (Rietveld et al., 1967; Jeffreys, 1968b).

But the considerable volume of work on flashed patterns is very difficult to interpret because the VEPs include large components due to change of luminance, as well as the pattern-related components. Some authors have attempted to eliminate the luminance-change components by subtracting from the flashed pattern VEP the VEP to homogeneous flash (Rietveld et al., 1967; Jeffreys, 1969) or to flashed defocussed pattern (White, 1969), a procedure that resulted in a simple diphasic or triphasic VEP. This assumes that there is a linear relationship between brightness-related and pattern-related components of the VEPs, and there is indeed evidence for the validity of such an assumption (Jeffreys, 1968a, b), although not under all stimulus conditions (van der Tweel et al., In Press). The latter facts strongly suggest that the brightness-related and pattern-related VEP components are generated in neural mechanisms that are largely independent of each other.

The above-mentioned subtraction process was used by Jeffreys (1969) for an investigation of the variation of pattern-related VEP components with stimulus patterns (Fig. 1.1.1.). A pattern of continuous parallel straight lines was found to be less effective than an array of broken lines for producing large VEPs. In general, patterns rich in high-order pattern-features such as corners and discontinuities produced larger VEPs.



Variation of "pattern-related" EP components with stimulus patterns T.1-T.8 (left-hand column) for 4 subjects. The wave forms shown were obtained by subtracting the EP to the flash-presented blank field from that obtained to the flash-presented patterned field. (To obtain a similar intensity distribution for the blank field in each case, the appropriate pattern was placed behind the opal glass screen.) Typical "blank flash EP's" are shown in the upper traces.

Fig.1.1.1. (After Jeffreys, 1969).

Similar, though less detailed, conclusions were previously reached by Rietveld et al. (1967), who suggest that corners are more effective stimuli when the corner angle is acute, rather than obtuse.

It has been claimed that the regularity of the pattern is a very important parameter (Beatty & Uttal, 1968; Beatty, 1969). They reported that the VEP produced by regular line or dot patterns was reduced if the patterns were made even slightly irregular. But Jeffreys (1969) found no such effect. Beatty & Uttal did not take any measures to eliminate brightness-related components from the VEPs, and this may, perhaps, be the cause of the discrepancy.

(b) Constant luminance pattern VEPs.

Although the process of subtracting the blank VEP from the flashed pattern VEP to give an uncontaminated pattern-related response seems to be valid under many conditions, a more satisfactory and direct method for avoiding brightness-related VEP components is to use a stimulus which does not involve any change in mean luminance. Three main kinds of constant-luminance patterned stimulus have been used. (i) Pattern-appearance (Jeffreys, 1968a, b, 1969, 1970a, b; Rietveld & MacKay, 1969a, b; van der Tweel, Regan & Spekreijse, 1971). (ii) Pattern-disappearance (van der Tweel et al., 1971). (iii) Pattern contrast-reversal. This form of stimulus has been used widely both with grating patterns (Johnson et al., 1966; Cobb et al., 1967b; Riggs & Whittle, 1967; Campbell & Maffei, 1970; Maffei & Campbell, 1970; May et al., 1971) and also with checkerboard patterns (Spekreijse, 1966; Cobb et al., 1968; Michael & Halliday, 1970; van der Tweel et al., 1971; Regan & Richards, 1971).

(b.1.) Pattern-appearance VEPs.

VEPs to pattern-appearance at constant luminance are essentially triphasic, if stimulation is limited to the upper or lower half of the visual field. The peak latencies are at approximately 80,110 and 180 msecs, but may vary according to the stimulus parameters. For lower half-field stimulation, the first and third peaks are positive and the second peak is negative; but for upper half-field stimulation the polarities are usually reversed (Jeffreys, 1970a, b, 1971). (Such polarity-reversal also occurs with VEPs to checkerboard pattern-reversal (Halliday & Michael, 1970). The three peaks in the pattern-appearance VEPs do not have identical scalp distributions. Detailed studies of the first two peaks for different 30° and 45° sector and semi-annular fields suggest, on the basis of a dipole model, that the first peak originates in striate cortex, the second in extra-striate cortex, both components reflecting activity which is negative at the cortical surface (Jeffreys, 1970b, 1971). The dipole model satisfactorily explains the polarity-reversal between upper and lower half-fields.

Not only do the components (peaks) have different scalp distributions, they also respond differently to various stimulus parameters. In particular, the second and third components are considerably reduced by prolonged pre-exposure of a pattern, if the form and orientation of the stimulus pattern and pre-exposure pattern are similar, but the first component is not greatly affected. (Jeffreys & Axford, unpublished data). For this reason, if the stimulus repetition rate is

high, the later VEP components are reduced if the pattern-appearance time is greater than about 50 msecs.

(b.2.) Pattern-disappearance VEPs.

There is only one published report concerning VEPs to pattern-disappearance at constant luminance (van der Tweel et al., 1971). Using low-contrast patterns, they found that the pattern-disappearance VEPs were unipolar and of opposite polarity to the main component of the pattern-appearance VEPs (probably the second of the three components identified by Jeffreys). The amplitudes of the pattern-disappearance VEPs were greatly reduced if the rate of change of spatial contrast at transition was reduced. In this respect, the pattern-disappearance VEPs differed from pattern-appearance VEPs, for the latter were not greatly affected by variations in the rate of change of contrast.

VEPs to the disappearance (and also to the appearance) of dot patterns have been studied by Harter (1971), but in these studies there was no attempt to hold the luminance constant. Both the appearance and disappearance VEPs were markedly reduced by defocussing, and both were strongly dependent on the size and spacing of the dots. The most effective stimuli were smaller in subtense for the off-responses than for the on-responses. Lesevre & Remond (1970) have studied VEPs to the illumination and occlusion of checkerboard patterns. The responses were very complex, as one would expect since they did not eliminate brightness-related components. They noted that the off-response was smaller than the on-response.

(b.3.) Pattern contrast-reversal VEPs.

VEPs to checkerboard-reversal were first investigated by Spekreijse (1966). For small check-sizes (20') such VEPs were almost certainly caused by contrast-sensitive mechanisms for the following reasons.

(i) The VEP amplitude was very greatly reduced by defocussing.

(ii) The VEP was suppressed by placing thin black threads so as to obscure the reversing contours (for a check size of 10', a 20" width of thread was sufficient to completely suppress the VEP). But threads located along the middles of the squares had much less effect.

(iii) The checkerboard-reversal VEP amplitude was largely independent of temporal frequency up to about 20 reversal/sec, then greatly reduced for any further increase in frequency. This contrasts with VEPs to sinusoidally modulated luminance, which show resonance peaks at approximately 10Hz, 50Hz and sometimes 16Hz (van der Tweel & Lunel, 1965; Regan, 1968). In Spekreijse's (1966) experiments, the contrast varied sinusoidally, but a qualitatively similar dependence on frequency and resolution of the pattern has been observed for step-modulated checkerboard VEPs (Cobb et al., 1967b, 1968).

The above results are for check sizes of 20' or less, but there is evidence that the contrast-specific components of the checkerboard-reversal VEP may be seriously contaminated with other kinds of component for check sizes above 20' (Regan, 1971). Firstly, although defocussing the retinal image attenuates the VEP for check sizes below 20', it can substantially increase the VEP for larger

check-sizes (Regan & Richards, unpublished observations). Secondly, VEP suppression due to placing thin black threads over the reversing edges is only effective for check sizes less than approximately 20' (Spekreijse, 1966).

This suggests that the checkerboard-reversal VEPs studied by Michael & Halliday (1971), and Halliday & Michael (1970), using a 50' check size, may well have been contaminated by components not contour-specific. Nevertheless, the main components of the above VEPs showed polarity-reversal between upper and lower half-field, as reported for pattern-appearance VEPs by Jeffreys (1969), which suggests that they were pattern-specific. For, with homogeneous flash stimulation, polarity-reversal effects between the upper and lower half-fields have been reported only for small-field stimulation, and even then only for certain VEP components (Schreinemacher & Henkes, 1968); for visual fields of the size used by Michael and Halliday (i.e. 7-9° radius), such polarity-reversals do not apparently occur, although the differences in the VEPs between upper and lower half-fields stimulation is greater than between right and left (Rietveld et al., 1965).

Aspects of research on pattern-evoked potentials will be further reviewed in relation to eye-movements (1.1.3), cortical topography (1.1.4), and motion (1.1.5), and in connection with the relationship between VEPs and single unit physiology and psychophysics (section 1.4.).

1.1.3. Eye-movement VEPs.

Saccadic movements of the eyes over a patterned field produce lambda-shaped waves in the raw EEG called "lambda waves" (Evans, 1952), which are localised over the parieto-occipital scalp. Averaged lambda waves, sometimes called "lambda responses" have been investigated widely (Gaarder et al., 1964; Barlow, 1964; Remond et al., 1965; Armington et al., 1967; Scott & Bickford, 1967; Barlow & Ciganek, 1969; Lesevre & Remond, 1970).

It seems that lambda responses are produced largely by displacements of the retinal image during eye movements, because the voltage-time waveform is very similar in VEPs due to object movement and in those due to eye movement (Barlow & Ciganek, 1968; Lesevre & Remond, 1970), and there is no significant difference between VEPs to active or passive saccades (Scott & Bickford, 1967). Again, the scalp distributions of lambda responses and pattern-displacement VEPs are very similar (Lesevre & Remond, 1970), and lambda waves recorded direct from the cortex in human patients have a triphasic or diphasic waveform (Chatman et al., 1960), similar to that reported from the scalp to pattern-appearance (Jeffreys, 1969).

Also, Armington et al., (1968) recorded VEPs to involuntary saccades over a grating pattern, and found that the VEPs were largest for bars subtending 9'-13', which is approximately the median amplitude of saccadic eye movements. They interpreted this as evidence that the VEPs were essentially pattern-displacement VEPs.

Nevertheless, it should be noted that the similarity between pattern-displacement VEPs and lambda responses is not quite perfect, (Barlow & Ciganek, 1968; Lesevre & Remond, 1970), and there is a small but measurable response even to saccades over a uniform dark field (Lesevre & Remond, 1970); evoked potentials to saccades in the dark have been reported also in cat cortex (Jeannerod & Sakai, 1970). So lambda-responses are probably pattern-displacement VEPs with minor non-visual components also involved.

Lesevre and Remond (1970) have found that lambda responses consist essentially of components due to the start and finish of the eye movements over the pattern. The presence of the pattern during the saccade does not seem to be important.

1.1.4. Evoked potentials and cortical topography.

In this section, the relationship between scalp-recorded VEPs and the large-scale cortical activity producing them will be discussed, with special reference to pattern-evoked potentials as these are particularly relevant to the present study.

(a) Pattern VEPs in monkey cortex.

There are unfortunately few data on pattern VEPs recorded directly from the cortex. VEPs to flashed patterns were recorded in the striate cortex of awake rhesus monkeys (Pribram, Spinelli & Kamback, 1967; Spinelli, 1967). The main VEP components had latencies between about 50 and 100 msecs and depended to some extent on the pattern used (circle or stripes). But the above experiments were primarily concerned

with higher functions, and provide little helpful information for interpreting human scalp-recorded VEPs.

Lambda waves (which probably include pattern VEP components) have been investigated in unanaesthetized monkeys (Hughes, 1964). They were found to be essentially biphasic at the cortical surface, first negative, then positive. The positive component is greater on the mesial surface of the occipital cortex, but the earlier negative component is greater on the lateral surface. There appear to be two main foci of activity on the mesial surface; one near the parieto-occipital sulcus, the other in the region of the calcarine sulcus. On the lateral surface there is one main focus of activity midway between the parieto-occipital sulcus and the occipital pole. Scott and Bickford (1966) found the lambda responses to be triphasic, however, whether recorded from humans, using scalp electrodes, or from monkeys, using multiple depth electrodes and subdural electrodes. The latencies of the three peaks appear to have been comparable with the latencies of the three components noted by Jeffreys (1970b, 1971) in pattern-appearance VEPs recorded from the human scalp.

(b) <u>The relationship between scalp activity and cortical surface activity.</u>

Cooper et al. (1965) found that although flash VEPs recorded from human subdura and scalp were similar when recorded over non-specific frontal cortex, they were dissimilar when recorded over specific occipital cortex. On the other hand, Vaughan has presented data from patients and monkeys that scalp-recorded VEPs to flash were

of similar form to the cortical potentials, although attenuated (MacKay, 1969). An intermediate position is that of Heath and Galbraith (1966), who reported fairly good agreement between scalp-recorded and cortically-recorded VEPs, but also noted that there was considerable spread to distant scalp electrodes. Such spread between scalp and cortex has the effect of averaging out cortical activity if it is highly localised, but not if it is more widespread (de Lucchi et al., 1962).

There is evidence, also, that the cortex, in generating VEPs, behaves as a dipole sheet (Fourment et al., 1965; Vaughan, 1969), which opens up the possibility of accounting for the distributions of the VEPs according to volume-conductor theory, using a dipole model. It has been argued by Vaughan that the brain medium can, for these purposes, be considered an isotropic, purely resistive medium (MacKay, 1969).

In particular, Jeffreys (1969, 1970a, b; 1971), Halliday & Michael (1970), and Michael & Halliday (1971) have proposed dipole models to explain the distribution of pattern VEPs. The matter has aroused some controversy.

Jeffreys (1969) reported polarity-reversal between upper and lower half-fields for all three components of the triphasic VEPs which are produced by pattern-appearance. He suggested that the polarity-reversal could be explained if the responses were generated in the calcarine fissure (striate cortex), since the upper and lower half-fields project to regions of calcarine cortex that are inverted with

respect to each other. For it is well known that regions near the horizontal meridian in the lower and the upper half-fields project to the roof and floor respectively of the calcarine fissure in man (Holmes, 1918, 1945; Teuber, Battersby & Bender, 1960; Brindley & Lewin, 1968), as in monkey (Talbot & Marshall, 1941; Cowey, 1964).

Halliday & Michael (1970) did not accept Jeffreys' explanation that the VEPs originated in the calcarine fissure. They used alternating checkerboards, stimulating different octants of the visual field, and found larger responses from the near-vertical octants than from the near-horizontal ones, and the polarity-reversals were most pronounced between upper and lower vertical octants. Since these octants are represented mainly outside the calcarine fissure (Holmes, 1918; Brindley & Lewin, 1968), they argued that another explanation for the polarity reversals was required. Moreover, both checkerboard-reversal VEPs and flashed-pattern VEPs were optimal about 5-7.5 cm anterior of the inion, whereas one would expect responses from striate cortex to be optimal within about 2.5 cm of the inion. Halliday & Michael (1970) therefore suggested that the VEPs were generated in extrastriate cortex, and came to the eventual conclusion that the polarity-reversal was due to the difference in orientation between the VEP-generating dipole sheets on the upper and lower surfaces of the occipital lobes (Michael & Halliday, 1971). It should, however, be emphasized that these results cannot be directly compared with those of Jeffreys (1969, 1970a, b, 1971) since the conditions of

stimulation and the resulting VEPs were very different.

Further work of Jeffreys (1970b, 1971) using sectors and semi-annular fields led him to conclude that the first component of the pattern-appearance VEPs did originate in striate cortex, polarity-reversal being caused in the manner previously suggested (1969); but that the second component was extrastriate in origin, polarity-reversal being caused by differences in the orientation of the VEP-generating dipole sheets in extrastriate cortex on the upper and lower surfaces of the occipital lobes.

1.1.5. Motion-evoked potentials.

Long before modern averaging techniques became available, Marshall & Harden (1952) recorded the EEG power spectrum and found, by this means, indications of cortical activity caused by the periodic expansion of circles generated on a cathode ray screen. They found that repetitive expansion of a circle at constant velocity was a much more powerful stimulus than flashing a stationary circle on and off. The brightness level of the stimulus was not an important parameter, and, indeed, changes in the power spectrum due to the stimulus could be detected even when the pattern brightness was only just above threshold. The sharpness of focus of the expanding circle was, however, a very important parameter, and even a slight decrease in pattern sharpness produced a noticeable attenuation in the analysed energy at the pattern frequency.

Since the advent of single unit recording, which demonstrated

the importance of stimulus motion for triggering single cells in mammalian cortex (Hubel, 1959; Hubel & Wiesel, 1962), the effect of motion has been a natural candidate for investigation in VEP research. Yet, in fact, comparatively little research has been done in this field.

MacKay & Rietveld (1968) found that the onset of vertical motion (at 2.3°/sec or 4.6°/sec) of a stimulus line produced a measurable VEP, and, very interestingly, the addition of a reference line enhanced the VEP. The degree of enhancement was inversely related to the distance between the two lines. It is unlikely that much of the response was caused by the removal of light from the fovea when the stimulus line was displaced, for there was no consistent asymmetry between the VEPs for fixation above and below the rest position. EOG readings indicated that transorbital potentials did not contribute significantly to the VEPs. A line raster was a more effective stimulus than a single line, and the VEP increased as the spacing between lines decreased within the range of spacings investigated (up to 3.5 lines per degree).

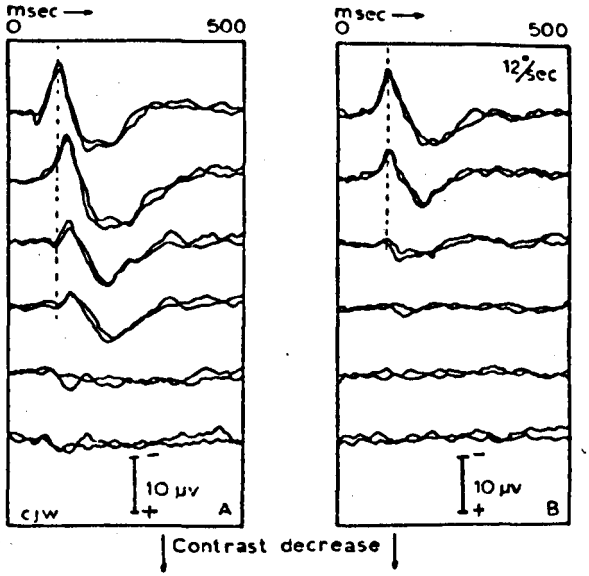
The above results were all concerned with the <u>onset</u> of motion of a line or line raster, but <u>reversal</u> of the motion of a line raster also produced a VEP. In this case the effects of varying the direction of motion were investigated, but the VEP showed no significant dependence on direction of motion.

MacKay & Rietveld considered that the nature of the technique

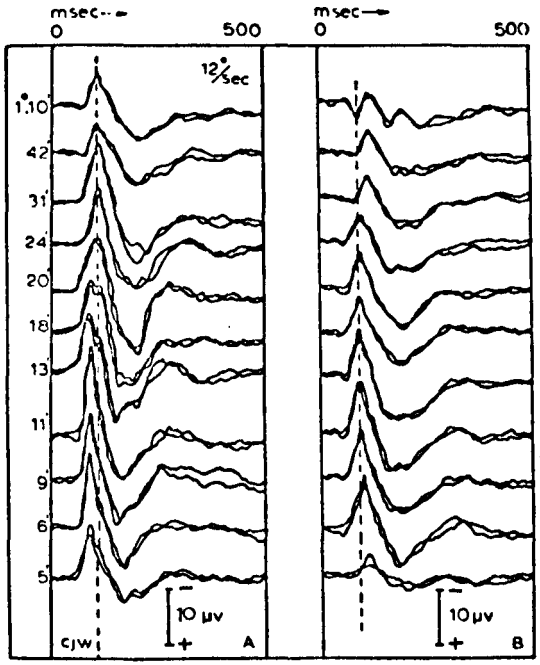
prevented the recording of signals indicative of steady velocity, so that it remained doubtful whether these VEPs reflected the activity of velocity-sensitive units.

Dawson, Perry & Childers (1968) compared VEPs to the scanning motion of an oscilloscope spot and diffuse flash. At low brightness levels, especially, the moving spot was a more potent stimulus than diffuse flash. Rather high speeds were used (29°/sec - 420°/sec), which is perhaps unfortunate as the available data from cortical single units in lower animals (Pettigrew et al., 1968; Wurtz, 1969a) as well as human psychophysical data (Sekular & Ganz, 1963; Sekular & Pantle, 1966; Richards, 1971) suggests that speeds within the range 2-20°/sec would have been the most effective for activating movement-sensitive mechanisms. The lowest speeds used by Dawson et al. produced the largest VEPs, which is at least compatible with their interpretation that movement-sensitive units were involved in producing the VEPs. EOG recordings gave no indication of eye movements elicited by the stimulus. No attempt was made to determine the extent to which movement-insensitive mechanisms may have been contributing to the VEPs.

Rietveld & MacKay (1969a, b) investigated VEPs to the reversal of direction of motion of patterned visual stimuli, and compared these with VEPs to the appearance at constant luminance of stationary patterns. These two forms of stimulation produced VEPs which were in some respects very similar, but there were differences too. Firstly, decreasing the pattern contrast greatly diminished both kinds of VEP;



a) Effect of contrast decrease on VEPs to pattern-appearance (left) and motion-reversal (right). (After Rietveld and MacKay,1969b).



b) VEPs to various check-sizes: motion-reversal VEPs (left), pattern-appearance VEPs (right). (After Rietveld and MacKay, 1969b).

Fig. 1.1.2

but it increased the latency of pattern-appearance VEPs and yet did not affect the latency of motion-reversal VEPs (Fig. 1.1.2a). Secondly, checkerboard pattern motion-reversal produced VEPs which included a negative double peak, in which the two components were differently affected by changes in check size, but pattern-appearance VEPs included no such double peak (Fig. 1.1.2b). Thirdly, the latency of motion-reversal VEPs varied much less over the scalp than did the latency of pattern-appearance VEPs. It was concluded that the differences between the VEPs to the two kinds of stimulus were sufficiently significant to indicate that different response mechanisms may have been involved. It will be argued in section 1.5, however, that the evidence for this (admittedly tentative) conclusion suffers from a number of subtle weaknesses.

There is some evidence for a VEP correlate to the perception of apparent motion when a checkerboard pattern is displaced a small distance (Regan & Spekreijse, 1970). Small (10') step displacements of the checkerboard produced a strong sensation of apparent movement and evoked a VEP. If the displacement was increased to 20' and 40' there was little or no illusion of movement and the VEP was reduced in amplitude.

1.2. The perception of movement.

The ability to respond to moving objects is essential for animals at every level of the evolutionary scale. Stationary objects can often be safely ignored, but a moving object may be a predator,

on the one hand, or prey on the other; and survival itself depends on an efficient and appropriate response in either case. Indeed, the visual systems of lower animals respond only to moving objects, and the extreme periphery of the human retina is likewise sensitive only to movement (Gregory, 1966).

Since the ability to respond to movement is phylogenetically very primitive, one might expect it to persist as an independent process throughout the evolutionary scale up to man. Certainly this seems to be the case at the level of eye movement control, for there is strong evidence in favour of independent position-control and velocity-control feedback systems for human eye movements (Fender & Nye, 1961; Rashbass, 1961; Starr, 1967). We now consider in some detail the evidence for independent processing of movement information at the perceptual level.

1.2.1. Movement perception as an independent process.

In the context of a discussion on the after-effect of seen movement, Mach (1875) states: "In a sensation process, we may assume as many different physical processes as there are psychically distinguishable different sensation-qualities". MacKay (1961a) likewise regards the movement after-effect, which appears as movement without change of position, as evidence 'that the visual system incorporates detectors of motion as such', since it seems reasonable to infer that the effect is due to the movement-detecting system becoming adapted just as the brightness and colour detecting systems can become adapted

(see Wohlgemuth, 1911). Also, he found that continuously lit objects yielded considerably lower thresholds for retinal image displacement than did stroboscopically lit objects, suggesting that 'the visual mechanism has developed an enhanced sensitivity to "stroking" by the retinal image, as distinct from a mere displacement' (MacKay, 1961a). A related phenomenon is the more recent discovery that the movement after-effect is greatly weakened if the stationary surface against which it is viewed is stroboscopically lit (Anstis et al., 1963). The after-effect can, however, be produced by phi-movement (Wohlgemuth, 1911).

The above inference from the waterfall phenomenon that velocity and position are separately coded is supported by the fact that velocity discrimination is strongly dependent on luminance near threshold for a medium range of velocities, (Brown, 1955), whereas accuracy of localisation of target position is independent of luminance (Leibowitz et al., 1955). The product of luminance and exposure duration at the threshold for movement is constant for durations below 0.1 msecs, but for longer durations luminance is less important. Leibowitz (1955a) has suggested that the decreased importance of luminance at longer durations is due to indirect inference of velocity from position. He supports this interpretation by his discovery (Leibowitz, 1955b) that reference lines only affect the rate threshold for movement-detection when the exposure duration is long (several seconds).

Riddoch (1917) has argued that "movement may be recognised as

a special visual perception" on the grounds that missile wounds can abolish the perception of form in parts of the visual field where movement perception remains (see also Teuber et al., 1960). But Teuber (1960) points out that the retention of movement vision can be explained purely in terms of greater stimulation due to the wider angle of extent covered by the test stimulus, and the elimination of Troxler's effect (i.e. the subjective fading of the image of a stationary object located in the periphery of vision, while the subject fixates (Clarke, 1960).

Teuber's argument is strengthened by the fact that in parts of the visual field where form vision is abolished, there is always some distortion of movement-perception, normally an increase in apparent velocity (Bender & Teuber, 1949; Teuber & Bender, 1949). In general, it must be said that data from brain-damaged subjects is difficult to interpret in the present context, and no firm conclusions can be drawn from it concerning the relationship between movement-perception and other forms of perception.

The discovery of direction-selective single cells, discussed in the next section of this chapter, is suggestive of separate mechanisms for processing movement information. It would seem particularly significant that, in cortex of awake cat and monkey, two distinct classes of neurone have been reported; one optimally responsive to stationary stimuli, the other to moving stimuli (Wurtz, 1969a; Noda et al., 1971). But no direct conclusions about perception can

be drawn from these purely physiological findings. There are, however, psychophysical data which correlate with the single unit experiments; the luminance threshold for bars moving in a given direction is raised by pre-exposure with high contrast bars moving in the same direction, and less if the pre-exposure bars move in the opposite direction (Sekular & Ganz, 1963; Pantle & Sekular, 1968a, 1969; Sekular, Rubin & Cushman, 1968). It appears that there are two types of elements being saturated. One type is sensitive to the direction of motion and orientation, but is largely independent of contrast; the other type is sensitive to orientation but not motion-direction, and is more dependent on contrast (Pantle & Sekular, 1969). The saturation experiments suggest that the human visual system is more selectively tuned to line-orientation than to movement-direction (Sekular, Rubin & Cushman, 1968).

The above experiments suggest that movement information is processed separately from other kinds of visual information. But movement-processing cannot be completely separate. When viewing a moving object I do not merely see movement and an object; I see a moving object. The notion of separate processing of movement information must never, therefore, be taken to imply a complete divorce between movement-processing and other kinds of brain function. Indeed, MacKay's (1957a, b) discovery that regular stationary (even retinally stabilised) patterns produce a moving "complementary after-image" is evidence that there is interaction between movement-processing and the processing of orientation and spatial periodicity.

1.2.2. The location of the processes underlying movement perception.

It would be very naive to attempt to locate the processes underlying the perception of movement in any particular area or areas of the brain, for the whole pathway between retina and motor mechanisms with all its many feedback loops is presumable involved. Nevertheless it is likely that some areas of the brain contain mechanisms that are directly concerned with the coding and processing of movement information, and it might be possible to locate these specialised mechanisms. In particular, it is very relevant in this evoked potential study to consider whether, and in what sense, movement-processing is likely to occur in the cortex.

Cortical lesions can distort or even abolish movement perception (Werner & Thuma, 1942; Teuber & Bender, 1949), which strongly suggests that the cortex does play a significant role in the perception of movement.

There is a parallel to this in the results of electrical stimulation of areas 17, 18 and 19 in epileptics. Whichever area was stimulated, coloured shapes were frequently seen, and more often than not they were moving (Penfield & Jasper, 1954; Penfield & Rasmussen, 1957). On the other hand, the results of Brindley & Lewin (1968) were strikingly different. They found that stimulating area 17 produced white phosphenes that were always stationary unless the subject, who was blind, moved her eyes. There are scarcely any data on direct stimulation of the visual system below the cortex, but Penfield & Rasmussen (1957) report one case of a patient who saw

a moving blue disc when stimulated by an electrode which was probably in the optic radiation or optic tract. It is not clear, however, that the movement-sensation was not due to eye movement. In view of the contradictions it would seem unwise to regard the stimulation experiments as evidence for or against the existence of movement-processing mechanisms in the visual cortex.

Ablation studies are a standard method for localising visual function, but it is often difficult to interpret these unambiguously as there are important fibre connections between cortex and colliculi, with complicated interaction between the two (Wickelgren & Sterling, 1969; McIlwain & Fields, 1970). Moreover, Sprague (1966) found that unilateral removal of the entire occipito-temporal neocortex in cat produced total contralateral hemianopia, as judged by the animal's visually guided behaviour; but removal of the superior colliculus contralateral to the cortical lesion restored vision. Also, many of the ablation studies have been performed on lower mammals, in which the cortex plays a lesser role than in man.

The experiments of Hamilton & Lund (1970) avoided the complications mentioned above, and used monkeys so that the results are probably applicable to man. They found that monkeys with sectioned optic chiasm and corpus callosum were incapable of interocular transfer of discriminations based on direction of movement. Control monkeys, with only the optic chiasm cut, did show transfer to the untrained eye. Hamilton & Lund conclude that discrimination of movement is a function

strongly dependent on the cortex. Complementary to this finding is that of Anderson & Symmes (1969) that the ability of monkeys to detect movement is not affected by collicular lesions, although such lesions do produce a largely temporary impairment of the ability to discriminate rate of movement.

These findings emphasize the importance of the cortex for movement perception, but it must be added that monkeys deprived of striate cortex can detect and reach for moving objects much better than they can for stationary ones. They cannot, however, track moving objects, although they can fixate (Humphrey & Weiskrantz, 1967). The residual vision in the de-striate monkeys is probably mediated via the collicular pathway, for, in monkey, area 17 probably receives the entire geniculo-cortical projection (Cowey, 1964; Cragg, 1969).

Many authors have tried to locate the movement detectors whose saturation, one would assume, causes the MAE. The fact that the effect can undergo interocular transfer has often been thought to imply a central origin, but Wohlgemuth (1911) pointed out that this does not necessarily follow, "for, as there is an after-effect in the subjective field of the closed eye, the contents of this probably fuse with the open eye". (p.28.) Barlow & Brindley (1963) therefore tried the effect of pressure-blinding the stimulated eye and found interocular transfer still took place, implying that the effect is not retinal. The matter is open to some debate, however (Pickersgill, 1963; Pickersgill & Jeeves, 1964; Scott & Wood, 1966).

Other evidence suggests that there may be both central and peripheral components to the MAE. If the two eyes are stimulated with opposite movements, there is no MAE if both eyes are kept open during the test period; but if one eye is shut there is an MAE appropriate to the stimulation of the open eye (Wohlgemuth, 1911; Anstis & Moulden, 1970). Anstis & Moulden conclude that 'this MAE must be retinal, or at any rate peripheral to the point of binocular fusion'. On the other hand, dichoptically produced movement causes an MAE when monocular viewing of the stimulus gives no sensation of movement (Papert, 1964; Anstis & Moulden, 1970). The investigators concluded that this effect must be central to the point of binocular fusion.

The above experiments are certainly suggestive of the conclusions which the authors claim; but they apparently make the tacit assumptions that there is a clearly definable stage of binocular fusion at which all distinctions between monocular inputs are discarded, and that processing is serial with no feedback between levels. Almost certainly neither assumption is true, for cortical and collicular cells are often unequally influenced by the two eyes (Hubel & Wiesel, 1962; Sterling & Wickelgren, 1969); and there is evidence of feedback between different levels in cortex (Creutzfeldt & Ito, 1968) and midbrain (Lorente do No, 1938).

None of the experiments on the MAE mentioned above provides evidence on the relative importance of the retino-cortical and retino-collicular pathways in producing the MAE. But Richards (1971) found

that spirals of about 3° in diameter were most effective for producing the spiral after-effect, suggesting that the receptive fields for motion-detection were typically of that size. By analogy with single unit data from animals he argued that such large receptive fields were located in the superior colliculi. Also, Richards & Smith (1969) argue against the cortex as the site of the MAE, because an MAE generated in a small part of the visual field, does not change size with eye convergence, whereas a scotoma due to a cortical lesion does. They suggest the midbrain as an alternative site. It would be wise, however, to regard this evidence cautiously until more is known about the mechanisms of change of apparent size during convergence. Moreover, a cortical role in the MAE is implied by the discovery (Dixon & Jeeves, 1970) that interocular transfer of the MAE is greatly reduced in acallosal subjects.

In summary, it would seem very likely that, in man, the visual cortex plays an important role in the perception of motion; but there is evidence that the superior colliculus is involved too.

1.2.3. The importance of reference contours.

All real movement is relative, and the perception of such movement requires a decision as to which object is the stationary reference and which is actually moving. The careful work of Duncker (1938) indicates that we tend to regard the largest objects as stationary. For example, a spot viewed on a screen appears to move if the screen is moved while the spot is in fact stationary. Also,

Gibson (1966) and MacKay (in press) have argued that the visual system probably works on the null hypothesis that rigid motions of the whole visual field are caused by movements of the subject, whereas movements of small objects relative to the rest ofthe visual field are caused by movements of the object. There is physiological evidence that the same distinction is used even by the lowly cricket (Palka, 1969).

This should be borne in mind when interpreting evoked potentials to rigid movement of a complex visual field, as reported initially by MacKay & Rietveld (1968) and Rietveld & MacKay (1969a, b), and investigated further in this thesis. Indeed, MacKay & Rietveld (1968) did find that VEPs to the onset of motion of a single line were enhanced by the addition of a reference line, and depended on the relative velocity between two stimulus lines more than on their absolute velocities. Single units in cat visual cortex are likewise sensitive to the presence of a stationary landmark, and this need not be within the receptive field. A landmark can cause either an increase or a decrease in the response to an oscillating light-dark edge (Jones, 1970). Also, McIlwain (1964) has observed interaction between remote receptive fields of units in cat optic tract.

The lower threshold for perceived movement is not, however, greatly affected by the presence of a reference line if the moving target is only briefly exposed (125 msecs), but, for exposure durations of several seconds, a reference line reduces the threshold velocity (Leibowitz, 1955b). This is speculatively interpreted as evidence

that at longer exposure durations motion is inferred indirectly from position (see section 1.2.1.).

1.3. Single unit responses to the motion of a visual stimulus.

If physiological sense is to be made of human scalp-recorded evoked potential studies, they must be understood in relation to the underlying neural events; and studies on single units in the brains of lower animals provide some of the most important data on these events, notwithstanding the important differences between species. It is not possible, in the present state of knowledge, to directly relate evoked potentials to single unit activity (sub-section 1.1.4); but, even so, single unit studies provide essential clues to possible principles of the coding and processing of information in the brain, and suggest stimuli which are likely to be fruitful in evoked potential experiments. In addition, certain quantitative data (e.g. optimal stimulus velocity, average receptive field size etc.) are likely to be of some relevance to human evoked potentials (especially if the single unit data are from monkey - there are scarcely any from man).

For these reasons, single unit studies relating to the processing of movement information are of major relevance to this thesis, and will be discussed in some detail.

Movement-sensitive cells are normally selectively sensitive to one particular direction of stimulus motion, called the "preferred" direction. If a cell responds vigorously to motion in the preferred direction, but gives little or no response in the reverse (null) direction it is termed "direction-selective".

Direction-selective cells are widespread throughout the visual systems of many animals. They have been reported even as low as the retina in such animals as pigeon (Maturana & Frenk, 1963); goldfish (Jacobson & Gaze, 1964); frog (Lettim et al., 1959); and rabbit (Barlow & Hill, 1963a, b). But in animals with pronounced binocular vision, such as cat and monkey, direction-selective cells are rare in retina and lateral geniculate nucleus (LGN) (Hubel & Wiesel, 1960a, b), although numerous in cortex and superior colliculus (Hubel & Wiesel, 1962, 1965, 1968; Sterling & Wickelgren, 1969).

In this summary, the single unit physiology of vision will be reviewed for rabbit, cat, monkey and man, with special reference to movement-sensitivity. Greater attention will be paid to data from monkey and cat than to data from rabbit, as the visual systems of the former animals are more similar to the human visual system. Also, emphasis will be laid on cortical data, for it may be assumed that human scalp-recorded VEPs are generated mainly in the cortex (subsection 1.1.4).

1.3.1. Rabbit.

Right at the outset of this discussion of rabbit neurophysiology it is important to clarify what relevance it has to human brain processing. Certainly rabbit brains are very different from human brains, but, because of the greater simplicity of the rabbit visual system, it has been possible to elucidate a number of key principles concerned with movement-vision in rabbit, which may be applicable also in man; and many of these principles have not been apparent from studies on higher

mammals.

Rabbit retina.

Direction-selective units were first recorded in rabbit retina by Barlow & Hill (1963a), who found that reversing the stimulus contrast did not affect the preferred direction. In a more recent study involving a sample of 762 units, some 25% were found to be direction-selective (Oyster, 1968).

Barlow & Levick (1965) examined the organisation of direction-selectivity within receptive fields, and this has led them to propose a possible mechanism, illustrated in Fig. 1.3.1. A stimulus moving in the null direction inhibits each bipolar cell through a horizontal cell; if the timing is right this will prevent the cell from responding when the excitatory input arrives; but for motion in the preferred direction the excitatory input arrives well before the inhibiting one, and the bipolar cell will respond. This model correctly predicts, among other things, that the preferred orientation is unaffected by reversing the contrast between stimulus and background, and that there is no response at all to motion in the null direction. Dowling, Brown & Major (1966) have since provided confirmatory evidence of horizontal cell to bipolar cell synapses in electron-microscope studies.

Now in fact there are two distinct types of direction-selective retinal ganglion cell, giving on and on-off responses respectively to localised light flashes (Oyster & Barlow, 1967; Oyster, 1968). Barlow & Levick's theory applies to the on-off type, which is four times as

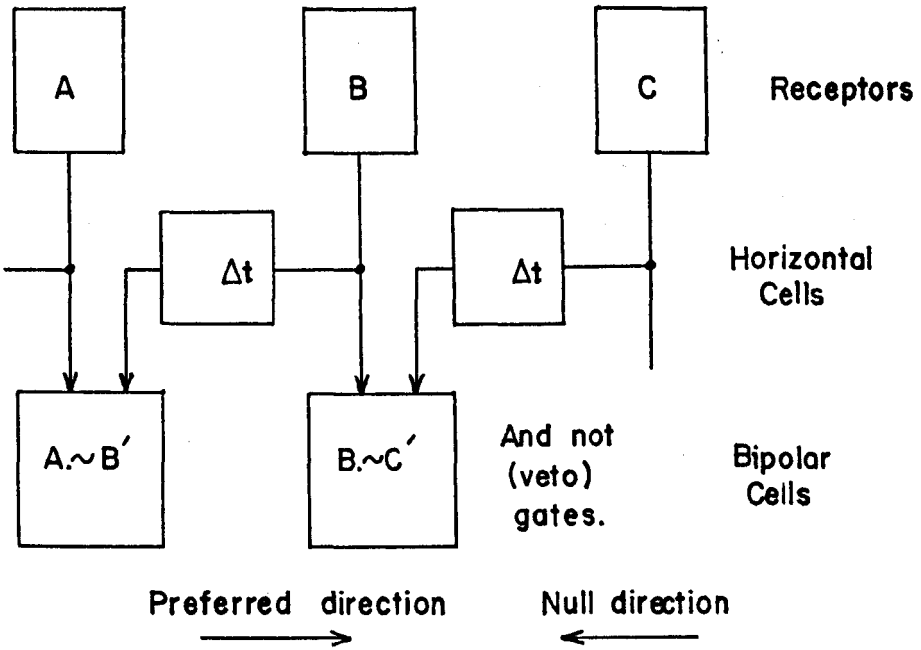


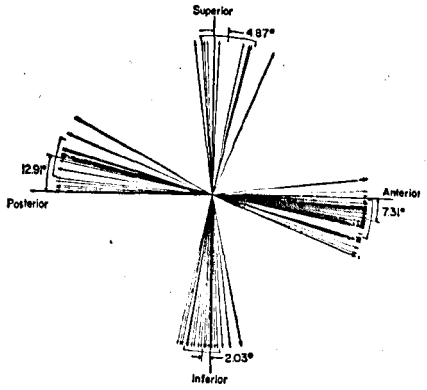
Fig.1.3.1. Barlow & Levick's model for directional-selectivity in rabbit retinal ganglion cells. (After Barlow & Levick, 1965).

common as the on-type. On-type units are maximally selective to one of only three directions of movement, but the on-off type units are maximally selective to one of four (Fig. 1.3.2). These four directions correspond to the directions of image motion produced by contraction of the four rectus eye muscles. This led Barlow & Oyster (1967) to suggest that the on-off type units were involved in the reflex control of eye movements, and might provide error signals to a visual servo system for minimising retinal image motion.

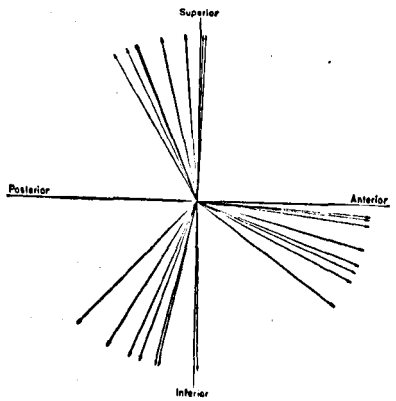
Also suggestive was the early finding that prolonged stimulation of cells in the preferred direction was followed by a period of suppressed spontaneous activity, for this may be a physiological correlate of the waterfall effect (Barlow & Hill, 1963b).

Rabbit lateral geniculate nucleus and cortex.

The retina-LGN-cortex pathway is by far the most important visual pathway in primates, and even in rabbit it is very important. Direction-selective units were first recorded in rabbit LGN by Arden, 1963; but probably the most interested finding was that of Levick et al. (1969), who reported that LGN neurones signalled movement direction more precisely than did their retinal counterparts. They presented evidence suggesting that this arose from the interaction of inputs from at least two retinal cells, one excitatory, the other inhibitory, whose preferred directions were 180° apart. One must interpret these results cautiously, however, for the effect of anaesthetic on rabbit LGN units has been shown to be very important. Stewart et al. (1971) reported that 19% of units



a) Distribution of the preferred directions of 79 'on-off' direction-selective units.



b) Preferred directions of 23 'on' type direction-selective units.

Fig.1.3.2. (After Oyster & Barlow,1967).

showed direction-selectivity in rabbit anaesthetised with nitrous oxide, but only 3% in awake, paralysed rabbit.

It appears that there is a great variety of cell types in rabbit visual cortex (Arden et al., 1967). Some respond also to non-visual stimuli. Many are direction-selective, but this property is not always constant throughout the receptive field. Some field sizes are very large (as much as 75°), a property also found in the superior colliculus.

Rabbit superior colliculus.

Little work has been done on the superior colliculus in the rabbit; but Hill (1966) identified several types of neurone, including direction-selective cells with very large receptive fields, up to about 25° in diameter, which is much larger than in the retina. Hill suggests that many retinal cells must converge on each of these large-field cells in the colliculus.

An alternative explanation would be that the large receptive fields are mediated via the cortico-collicular pathways, and this explanation has been advanced in the case of cat by Wickelgren & Sterling (1969). However, Masland et al. (1971) found no change in rabbit superior colliculus receptive field resulting from cortical lesions.

1.3.2. Cat.

Cat retina and lateral geniculate nucleus (LGN)

In the cat, as in other animals with binocular vision, there is little evidence of direction-selective units in the primary visual

pathway below the cortex. Most cells in the retina and LGN have a circular concentric centre-surround organisation (Kuffler, 1953; Hubel & Wiesel, 1960a, 1961). Nevertheless, Stone & Fabian (1966) and Spinelli & Weingarten (1966) have reported a very few direction-selective units in cat retina, and Kozak et al. (1965) report five more in the LGN, comprising about 4% of their sample. On the other hand, Hubel & Wiesel (1960, 1961) did not find any direction-selective units in cat optic tract or LGN, and Hubel (1963) points out the danger of confusion arising through recording from fibres just dorsal to the LGN instead of from the LGN itself, since some of these fibres may be corticofugal.

Cat thalamic nuclei other than LGN

There are few relevant data from these nuclei, but Kingston, Vadas & Bishop (1969) studied single units in various areas of the cat mesencephalon, and found that many of the units in the pulvinar and the lateral-posterior nucleus of the thalamus were direction-selective.

Cat visual cortex.

Hubel & Wiesel (1965) have shown that visual areas I and II, initially mapped out physiologically by Talbot & Marshall (1941) and Talbot (1942) respectively, are coextensive with anatomical areas 17 and 18 (Otsuka & Hassler, 1962). They have also identified a new area, visual III, that is coextensive with anatomical area 19.

Direction-selective cells have been found in all these areas, and also other parts of the visual cortex which will be described at the end of this section.

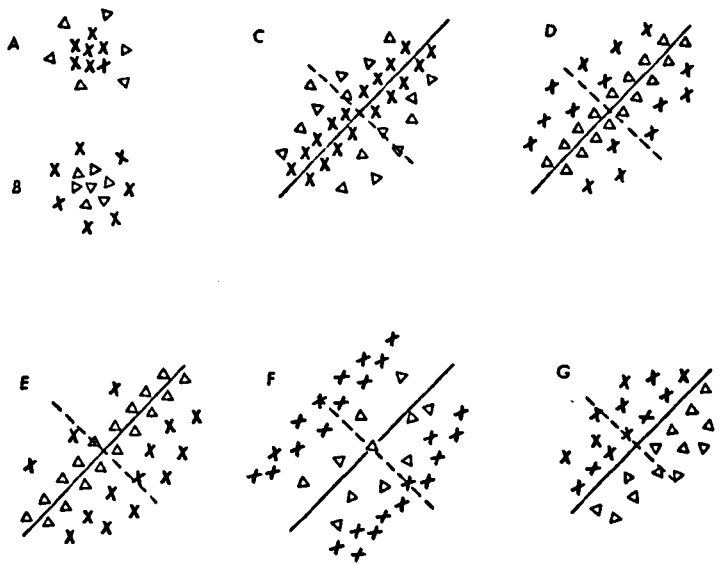
Area 17 (The Striate Cortex)

Direction-selective units are universally reported in striate cortex (e.g. Hubel, 1959; Hubel & Wiesel, 1959, 1962; Baumgartner et al., 1964; Campbell et al., 1968; Creutzfeldt & Ito, 1968; Pettigrew et al., 1968).

Hubel & Wiesel (1962, 1965) have identified a hierarchical organisation in the cat retino-cortical system: centre-surround cells in the retina converge on a second kind of centre-surround cell in the LGN, which is less sensitive to brightness and correspondingly more specific to contrast. Probably each geniculate on-centre cell receives its main excitatory input from one on-centre optic tract fibre and its inhibitory surround from several off-centre fibres (Singer & Creutzfeldt, 1971). These, in turn, converge on 'simple cortical cells' with rectangular receptive fields (Fig. 1.3.3). The receptive field regions are probably compounded by inputs from geniculate cell field-centres (Hammond, 1971).

The simple cells probably synapse onto complex cells (Denney, Baumgartner & Adornaji, 1968), which in turn probably synapse onto lower order hypercomplex, then higher order hypercomplex. These findings are very well known, and will only be discussed in detail insofar as they relate to the processing of movement information.

Simple, complex and hypercomplex cells are all found in striate cortex, but only complex and hypercomplex cells are known to exist in extrastriate (Hubel & Wiesel, 1962, 1965, 1968). All these types of cell are orientation-selective.



Common arrangements of lateral geniculate and cortical receptive fields. (*A*) "On"-centre geniculate receptive field. (*B*) "Off"-centre geniculate receptive field. (*C–G*) Various arrangements of simple cortical receptive fields. ×, areas giving excitatory responses ("on" responses); △, areas giving inhibitory responses ("off" responses). Receptive-field axes are shown by continuous lines through field centres; in the figure these are all oblique, but each arrangement occurs in all orientations.

Fig.1.3.3. (After Hubel & Wiesel, 1962).

There is a columnar organisation in the visual cortex; cells of the same eye preference tend to be clustered in columns perpendicular to the cortical surface, and cells responding to a common orientation form a second kind of column. The two systems seem to be independent (Hubel & Wiesel, 1962). Yet another system involves columns of binocular cells responding to a common depth (Blakemore, 1970). These results have interesting correlations in the histological findings of Colonnier (1964).

Hubel & Wiesel, (1962) found that a moving stimulus was very potent, "probably because of the synergistic effects of leaving an inhibiting area and simultaneously entering an excitatory area". About half the cells respond when the movement is in one specific direction (direction-selective), but they believe this "could usually be accounted for by an asymmetry in flanking regions". Pettigrew et al. (1968) deny this, however; they are emphatic that the direction-selectivity cannot be explained in that way, although they do not discuss what the mechanism is.

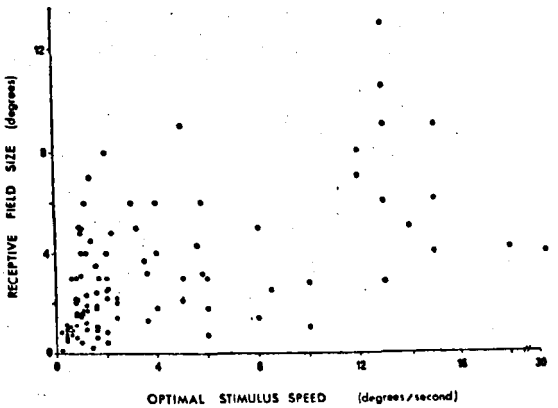
Creutzfeldt & Ito (1968) have attempted an analysis of the functional synaptic organisation of striate cortex neurones using intracellular or quasi-intracellular recording. They have studied spike activity and PSP's simultaneously. They find that in most movement-sensitive cells, only one part of the receptive field responds to movement and this is usually an off-excitation area. They also provide evidence that there are non-primary fibres converging on the

cortical cells in addition to the primary fibres from the LGN, and they have identified long-latency inhibitory synapses which may be involved in velocity-processing. Nevertheless, they do not propose any general model of direction-selectivity comparable to that of Barlow & Levick (1965) in the rabbit.

The most systematic data on the optimal speed for moving stimuli was provided by Pettigrew et al. (1968), (Fig. 1.3.4 and Table 1.3.1) but, as they point out, the criterion for optimal speed must be carefully defined. Judged subjectively by ear, the optimal velocity for most units was less than 6°/sec; but if the peak rate of firing was taken as criterion, the optimal speed was very much greater. This ambiguity must not be forgotten in any comparison between optimal speeds for evoked slow potential responses and single unit responses.

The receptive fields of simple cells at $1\text{-}4^{\circ}$ from the centre of vision were normally between $1/2^{\circ} \times 1/2^{\circ}$ and $4^{\circ} \times 4^{\circ}$, while complex and hypercomplex receptive fields were typically about twice that size. (Hubel & Wiesel, 1968.) Field sizes tended to increase with distance from the centre of vision (Hubel & Wiesel, 1962), and with stimulus velocity (Pettigrew et al., 1968).

In most single unit experiments the animal is anaesthetised, but similar results have been obtained in unanaesthetised, unperalysed preparations by Hubel (1959) and Noda et al. (1971), who both found that stimulus motion was a particularly important parameter. But Noda et al. reported that there were two main classes of units: direction-



Plot of optimal stimulus speed against receptive field core size for all units. Slow speeds predominate and there is little correlation between the two variables

Fig.1.3.4. (After Pettigrew, Nikara & Bishop, 1968).

Table 1. *Distribution of response types of single cortical units based on response vs. time histograms generated by repetitive movement of specifically-orientated slit stimuli*

Response Type	No. of units	Mean r.f. core size	Mean optimal stimulus speed
Simple			
1. Unimodal	—	1.5°	2.0°/sec
Directionally selective	26	—	—
Asymmetrical	18	—	—
Symmetrical	4	—	—
2. Bimodal	—	3.1°	10.1°/sec
Modes separated by $< 3°$	10	—	—
Modes separated by $> 3°$	6	—	—
3. Central inhibitory	2	—	—
Complex	—	6.1°	5.6°/sec
Directionally selective	17	—	—
Asymmetrical	16	—	—
All units	99	—	4.0°/sec

Table 1.3.1. (After Pettigrew, Nikara & Bishop, 1968).

selective neurones responding optimally to moving stimuli constituted one class, but neurones in the other class responded optimally to a correctly oriented stationary grating. The stationary grating produced in these units a maintained discharge, a phenomenon not found with stationary stimuli in anaesthetized cats (Hubel & Wiesel, 1962). Eye movements may be responsible for the difference. These results of Noda et al. closely parallel those of Wurtz (1969a) in unanaesthetized, unparalysed monkey. Noda et al. interpreted them as evidence that the visual system has different channels for the perception of stationary and of moving objects.

Areas 18 and 19 (the pre-striate cortex)

The most obviously important physiological difference between the striate cortex and the pre-striate cortex lies in the proportions of simple, complex and hypercomplex cells. Simple cells predominate in area 17 (striate), complex cells in area 18, and hypercomplex cells in area 19. Complex and hypercomplex cells have been reported in all three areas; but simple cells are apparently restricted to area 17 (Hubel & Wiesel, 1965, 1968).

Hubel & Wiesel (1965) provide little data on optimal speed of movement, but merely state that in complex cells the most effective speed was normally between 0.1°/sec and 20°/sec. They do not define their criterion precisely, but state: "The rate of movement was usually an important variable, since the cell's firing frequency tended to fall off sharply if the rate was less or greater than some optimum".

The Clare-Bishop area

An additional visual area was identified in a strip occupying

the lower half of the medial wall of the suprasylvian gyrus by Clare & Bishop (1954) using evoked potentials. Anatomical studies have demonstrated projections to this area from LGN and from areas 17, 18 and 19 on both sides. The evidence is summarised by Hubel & Wiesel (1969).

Receptive fields of cells in this area are mostly similar to the complex and hypercomplex cells of areas 17, 18 and 19, but the receptive fields are larger and proportionately more cells are direction-selective (Hubel & Wiesel, 1969; Wright, 1969), so this area may well play an important role in the processing of movement information.

Anterior portion of middle suprasylvian gyrus

In this area also, direction-selective cells are found. It lies close to the Clare-Bishop area, but is anatomically distinct from it, and the receptive fields are reported to be similar to those in the superior colliculus (Dow & Dubner, 1969, 1971).

Cat superior colliculus

The superior colliculus of the cat has been studied extensively. It is known to receive retinotopic projections from areas 17, 18 and 19 (Hayashi, 1969; McIlwain & Fields, 1970) as well as an input direct from the retina. It is generally considered that its main function is in the mediation of eye movements and visually guided behaviour (Schneider, 1969; Sterling & Wickelgren, 1969).

About three quarters of the units encountered in the superior colliculus are direction-selective, and few respond well to a stationary stimulus. The direction-selectivity of the cells cannot be explained

purely in terms of asymmetry in the receptive fields, because reversing the contrast of the stimulus does not change the preferred direction. The most usual optimal velocity is about 10°/sec. (Straschill & Taghavy, 1967; Sterling & Wickelgren, 1969.) A high proportion of direction-selective cells respond optimally to horizontal movement towards the periphery of the visual field (Sterling & Wickelgren, 1969).

Sterling & Wickelgren (1969) point out that collicular cells are similar in many ways to cortical hypercomplex cells (Hubel & Wiesel, 1965) for both kinds of receptive field consist of an activating region from which responses can be obtained, and flanking antagonistic regions which suppress the response if the stimulus is too long. Moreover both types of cell may be binocularly driven, are direction-selective, and respond to a stimulus anywhere in the receptive field. However, collicular cells are less specific for direction, and are less sensitive to stimulus size and shape.

In the primary visual pathway there appears to be a hierarchical organisation, with several stages between the retinal cells and the hypercomplex cells (Hubel & Wiesel, 1965), but there seem to be no stages between the retinal cells and the collicular cells. (Sterling & Wickelgren, 1969). In view of this, it might be expected that the complexity of collicular cell responses is largely mediated via the cortico-collicular pathway (Wickelgren & Sterling, 1969); and these authors found that ablation or cooling of the areas 17, 18 and 19 destroyed the direction-selectivity of collicular cells and enabled them to respond with a sustained discharge to stationary stimuli. On the other hand,

no such effect was noted by Marchiafava & Pepeu (1966), or Hoffmann & Straschill (1971), whose results were comparable with those of Masland, Chow & Stewart (1971) in rabbit.

1.3.3. Monkey.

Direction-selective units have not been recorded in the retina or LGN of monkeys (Hubel & Wiesel, 1960b; De Valcis, Abramov & Jacobs, 1966; Wiesel & Hubel, 1966), but they have been reported in the cortex (Hubel & Wiesel, 1968, 1970; Gross et al., 1969; Wurtz, 1968, 1969a, b, c) and the superior colliculi (Humphrey, 1968).

Monkey striate cortex.

Cell properties in monkey striate cortex are similar to those in the same area of the cat, but the proportion of simple cells is less (Hubel & Wiesel, 1968). They found about 9% simple cells, 65% complex cells, 20% lower order hypercomplex and 6% concentric-surround-type (sample of 272 cells); but they were not certain that the latter category did not originate from LGN fibres. The 9% figure for simple cells is almost certainly an underestimate, as these cells are apparently very small, and electrode penetrations sometimes stopped before reaching the cortical layers where simple cells predominate. Receptive fields are smaller in monkey than in cat; between $1/4^{\circ} \times 1/4^{\circ}$ and $1/2^{\circ} \times 3/4^{\circ}$ for simple cells, and about twice as large in each direction for complex and hypercomplex cells.

About half the cells are direction-selective, as in the cat, and in both animals Hubel & Wiesel (1962, 1968) ascribe this property to receptive field asymmetry. Nevertheless, it has already been

mentioned that this is contested by Pettigrew et al. (1968) for cat, and in monkey it is contested by Wurtz (1969a).

Hubel & Wiesel's experiments were carried out under light anaesthesia, whereas Wurtz (1969a) used unanaesthetised monkeys that had been trained to fixate. The results were in many respects similar but in the unanaesthetised preparation there were two main categories of unit; one class gave a maintained discharge to a stationary stimulus, whilst the other responded best to a moving one (Wurtz, 1969a).

Wurtz (1969c) also found that image movement in one direction and eye movement in the opposite direction always produced identical responses. Some units responded best to velocities below 20°/sec and not at all to higher velocities, but others were responsive to velocities as high as 900°/sec, comparable with the velocity of saccades. Some gave an excitatory response at low velocities, but an inhibitory response at high velocities.

The functional architecture of monkey striate cortex does not appear to differ greatly from cat. Orientation columns and eye preference columns have been reported in both by Hubel & Wiesel (1962, 1968), who have also demonstrated eye preference columns in monkey anatomically using the Nauta method (Hubel & Wiesel 1969b).

Monkey extrastriate cortex.

The only report of direction-selective cells in monkey visual cortex outside area 17 is a paper by Hubel & Wiesel (1970) which is primarily concerned with binocular cells sensitive to depth. They have

identified depth-selective columns reported by Blakemore (1970) in cat.

About half the cells in monkey area 18 were depth-selective and could not be strongly activated monocularly. The rest were complex and hypercomplex similar to those in area 17.

Monkey inferotemporal cortex.

Neurones in monkey inferotemporal cortex have visual receptive fields, which are usually very large and almost always include the fovea (Gross et al., 1969). About half of these units respond preferentially to a particular direction of stimulus-movement, but in some binocular units the direction is different for each eye. The mean latency of optimal activity of these units is very large (198 msecs).

Monkey superior colliculus.

The superior colliculus of monkey has been neglected by neurophysiologists, but Humphrey (1968) recorded single units which differed from collicular units in cat and rabbit. In particular, the monkey units were not at all specific to direction of movement, although they did respond better to moving stimuli than stationary ones. Receptive fields varied in size from about 2° to 90°. The smaller fields were round, but the largest areas approximated to quadrants of the visual field. The lack of direction-selectivity is very striking, suggesting that in monkey the retino-collicular pathway may not be important for movement vision. Ablation of monkey superior colliculus does not impair movement-detection, but it does cause a deterioration in movement rate-discrimination (Anderson & Symmes, 1969), as mentioned in the previous

section.

1.3.4. Man.

Inevitably there are only limited data from single units in the human visual system, but Weinstein, Hobson & Baker (1971) have recorded single units from an isolated human retina that have similar properties to monkey retinal single units. This very tentatively suggests that there is no velocity processing at the retinal level in man. Marg, Adams & Rutkin (1968) have studied a small number of single units in the occipital cortex of awake humans, and here they do find direction-selective units. There is no obvious difference between their findings and those of Wurtz (1969a) in awake monkey, so extrapolation from monkey data to man is not without justification.

1.3.5. Implications.

From the above review, it is clear that direction-selective neurones are very widespread throughout the mammalian visual system. It would seem unlikely that all such neurones should be concerned with the perception of movement, and it may well be that many direction-selective units are involved in processes correlating with the perception of fixated stationary objects. For it is well known that a stationary retinal image soon fades (Ditchburn & Ginsborg, 1952), and recent evidence suggests that continuous movement of the retinal image, rather than a series of instantaneous jerks, is required to maintain vision (Gerrits & Vendrik, 1970). But the neurones involved here would probably correspond to those in cortex of awake unparalysed cat and monkey, which give a

continuous discharge to a stationary stimulus; and there remains a separate class of neurones, which are highly direction-selective and do not respond well to a stationary stimulus even in awake, unparalysed preparations (Wurtz, 1969a, Noda et al., 1971).

The latter neurones may play a number of different roles. They may be involved in the perception of movement. Or they may be involved in the feedback loop for fixation, as suggested by Hubel (1959), or for tracking. Indeed, Oyster (1968) has argued compellingly in favour of such a feedback role for the retinal on-off-type units in rabbit retina, and Pettigrew et al. (1968) have noted suggestive similarities between such cells and simple cells in cat cortex. It should be noted in this context that de-striate monkeys can fixate a stationary object, but cannot track a moving one (Humphrey & Weiskrantz, 1967).

Whatever the functional roles of direction-selective cortical neurones may be, they would seem to be very likely contributors to motion-reversal VEPs.

1.4. The inter-relationships between single unit activity, VEPs and psychophysics.

It has been argued (section 1.0) that much of the prospective value of VEP research is likely to derive from its relationship with single unit phenomena on the one hand, and with psychophysics on the other. Few such relationships have so far been demonstrated, and none for motion-evoked potentials, although the enhancement by a reference line of the VEP to motion-onset reported by MacKay and Rietveld (1968)

may have some connection with some of the psycho-physical effects of a reference line reviewed in sub-section 1.2.3.

In this section, the available data concerning the relationships between single unit activity, VEPs and psychophysics are briefly summarized.

1.4.1. The electrogenesis of VEPs.

The electrophysiology of single neurones is now comparatively well understood. This understanding has been achieved mainly through intracellular recording from peripheral neurones, especially motoneurones in the mammalian spinal cord, but such evidence as there is from the central nervous system suggests that central neurones function on essentially similar principles. The subject is reviewed in standard texts (e.g. Eccles, 1968).

The question to be dealt with in this sub-section is: what is the relationship between the electrical activity of single cortical neurones and the cortical evoked potentials? This question is of considerable relevance to this thesis, because one would wish to understand the relationship between motion-evoked potentials and the activity of motion-sensitive single units. But alas, the whole topic is extremely complex and not well understood, and it can only be dealt with briefly here. The comparatively simple related question as to how the cortical evoked potentials relate to scalp activity has been dealt with in sub-section 1.1.4.

It is claimed by Fox & O'Brien (1965) that there is a high

correlation between the probability of firing of a single cell and the local evoked potential waveform. This applies for both positive and negative components, whether early or late in the evoked response. It has been verified for VEPs to flash and for somatic evoked responses.

Despite such findings, however, it remains true that our knowledge of the relationship between single unit firing and macro-potentials at the cortical surface is very incomplete. Perhaps the most clearcut model was presented by Creutzfeldt & Kuhnt (1967), based on their study of evoked potentials in sensorimotor cortex of cat to electrical stimulation of the specific thalamic projection nucleus. According to this model, slow surface potentials reflect the summated post-synaptic potentials of "average" cortical pyramidal cells. Contra Amassian et al. (1964), the model does not invoke morphologically distinct generators to be responsible for different phases of slow wave activity. Synchronous depolarisation of cortical neurones produces a surface negative wave, and polarisation produces a positive wave; but a phase reversal between fast deep activity and that at the cortical surface can occur because of the relatively slow electrotonic spread of potentials along dendrites. Creutzfeldt & Kuhnt (1967) do not favour the hypothesis of transcortical dipoles to explain the surface potentials.

Very similar conclusions to those above were previously reached by John et al. (1964), who included the visual cortex in their study. They stressed the role of the apical dendrites in producing the evoked potentials. Depolarisation and hyperpolarisation were found to produce

respectively negative and positive surface potentials. Depolarised deeper layers in the cortex, however, acted as sinks to the more superficial apical dendrites and thereby produced positive components at the surface.

The above results were all obtained in anaesthetised cats, but more recently Creutzfeldt et al. (1969) studied the relationship between flash VEPs recorded from the surface of the striate cortex and the underlying single unit activity in unanaesthetised paralysed cat. The initial component of the first positive wave (15-30 msec latency) correlated with the discharge of on-centre afferent fibres, and the main component of this wave (30-50 msec) correlated with the time course of inhibition of cortical cells. The succeeding surface-negative wave (60-100 msecs) was apparently related to the late excitation of a high proportion of the cortical cells. It is regrettable that such data are not available for pattern-evoked potentials.

Finally, it should be added that glial cells apparently make an important contribution to the evoked potentials, since they become depolarised when neighbouring neurones are active (Castellucci & Goldring, 1970), and are electrically coupled to each other by a low resistance pathway which causes them to act like a single long conductor. (Kuffler et al., 1966.)

1.4.2. VEP correlates of psychophysical phenomena.

There is not space to review all the investigations which have been made into the relationship between VEPs and psychophysical phenomena.

Two classes of phenomena have therefore been selected: (a) perceptual suppression, and (b) the angular and spatial selectivities of the visual system to spatially periodic grating patterns. For these topics are probably the most directly relevant to the present thesis, partly because they both involve contour-related VEPs.

(a) Perceptual suppression.

Evoked potential correlates have been sought for several different classes of perceptual suppressions; in particular, saccadic suppression, binocular rivalry, and the subjective fading of a stabilized image.

It is well known that the detection thresholds for flash brightness and spot displacement are raised if a saccadic eye movement occurs within about 50 msecs of the visual stimulus (Ditchburn, 1955; Volkmann, 1962; Latour, 1962; Beeler, 1967). Michael & Stark (1967) observed that the flash VEP waveform was distorted if a saccade occurred at such a time that perception of the flash was suppressed. More recently, Duffy & Lombroso (1968) reported that the total energy in the flash VEP (they computed the time integral of the square of the voltage) was reduced if the flash occurred during the interval, relative to the saccade, during which suppression occurred. These experiments were regarded as providing electrophysiological evidence in favour of a central suppression mechanism for maintaining visual stability or preventing retinal blur. Doubt has been cast on such interpretations, however, by the more recent discovery (Richards, 1968; MacKay, 1970) that passive eye movements raise the visual threshold to about the same

extent as do active eye movements, and over approximately the same temporal range relative to the test stimulus. As MacKay (1970) pointed out, it is likely that the threshold elevation is caused by the disturbance of the visual system resulting from the sudden displacement of the retinal image, and it is questionable whether the existing evidence requires any further mechanism of suppression to be invoked.

Gross et al. (1968) found that the VEP to reversal of the contrast of a barred pattern at the moment of onset of a saccade was almost identical to the VEP to the saccade alone with no alternation of the bar pattern. They subtracted one VEP from the other to eliminate the effects of eye movements, and interpreted the resulting near-zero response as evidence for a central suppression mechanism specific to contours. But this involved the assumption that the eye movement response and the pattern-alternation response were independent, and it is very unlikely that this was so. Indeed, it is well known that VEPs to pattern-alternation and to movement of the eyes over the pattern yield very similar responses (Lesevre & Remond, 1970) suggesting that the same mechanisms are largely responsible for both. It would therefore seem more reasonable to interpret the similarity between the VEPs to saccades with and without pattern-alternation as an indication that both VEPs are caused almost entirely by the displacement of the retinal image, for this will be similar in each case. On this view, the data of Gross et al. (1968) constitute evidence against, rather than for, a central suppression mechanism. This latter interpretation agrees well with

MacKay's (1970) explanation of the psychophysical data of threshold elevation.

Several investigations have been made as to whether the phenomenon of binocular rivalry is accompanied by corresponding changes in VEP. Investigations using unstructured fields have usually produced only slight differences in VEP between the dominant and non-dominant phases of the stimulated eye (van Balen, 1964; Cobb et al., 1967a). Lansing (1964) found more substantial differences in the amount of EEG activity in a narrow frequency band centred on the stimulus frequency, but this was very near the alpha frequency and there is evidence that the differences were caused by changes in the background EEG, not in the VEP (Cobb et al., 1967a). Donchin & Cohen (1970) did find clear evidence of suppression, however, using as stimulus a flash viewed through a small, square aperture. They attributed their unusual result to changes in attention to the flash rather than directly to rivalry. It is possible, however, that the differences in the VEP between dominant and non-dominant phases were directly due to rivalry, for the VEP to small square flash may have included a relatively large contour-related component, and contour-related VEPs do seem to correlate with rivalry. Such correlations were first reported by Cobb et al. (1967b) and MacKay (1968b), who found that contour-related VEPs were almost totally suppressed during the non-dominant phases of the stimulated eye. Such results cannot be caused by changes in accommodation, for van der Tweel et al. (1971) found that rivalry over part of the visual field affected the VEP the same as if just that part of the field had been occluded. Contrary

to the above results, Riggs & Whittle (1967) found that the VEPs to an alternating barred pattern and to a flashed barred pattern did not significantly depend on the phases of binocular rivalry. But, as Regan (1971) has argued, the frequency of alternation of the pattern in these experiments was about 25 HZ, at which frequency the contour-related VEP components are very small (Spekreijse, 1966; May et al., 1971), but brightness-related VEPs may be large (Regan, 1968). Flash-stimulation with the barred pattern was carried out at a lower frequency (9.5 HZ), but the method of stimulation was inherently likely to introduce considerable brightness-related artifacts. Thus it is possible that the discrepancy between the results of Riggs & Whittle and those of other workers is due to the predominance of brightness-related, instead of contour-related, components in the VEPs studied by Riggs & Whittle.

A number of experiments have also been carried out to investigate whether there is any VEP correlate of the fading phenomenon which is known to occur under conditions of stabilized image (Ditchburn & Ginsborg, 1952). Lehmann et al. (1967) and Riggs & Whittle (1967) presented both a continuously illuminated stabilized target and also flashes of light to the same eye, and found that the VEPs to the flashes were the same during periods of fading and during periods of normal vision. The fact that the VEP was not suppressed during fade-out may be connected with the similar lack of suppression of brightness-related VEPs under conditions of monocular rivalry (see above). Riggs & Whittle (1967) did, however, also use a retinally stabilized alternating pattern, with no VEP suppression, but it has been argued (above) that the

frequency of stimulation (c 25 HZ) was too high for the production of true pattern-evoked potentials.

Although there are no reports of VEP suppression during the period of fading of a stabilized image, it has been found that there is a high correlation between the occurrence of alpha rhythm and subjective fading (Lehmann et al., 1965).

(b) The angular and spatial selectivities of the visual system to spatially periodic grating patterns.

Psychophysical experiments have shown that the contrast thresholds for the detection of gratings whose luminance profiles are rectangular or sawtooth waves can be predicted from the contrast thresholds for sinusoidal gratings by means of Fourier theory (Campbell & Robson, 1968). The contrast thresholds for aperiodic patterns can be predicted on the same basis (Campbell et al., 1969b). These results can be explained by the existence within the human visual system of linearly operating independent mechanisms selectively sensitive to limited ranges of spatial frequency (Campbell & Robson, 1968).

Much earlier, MacKay (1957a) suggested the existence in man of channels sensitive to orientation, on the basis of the orthogonal moving after-images produced by regular stationary patterns; and Sekular (1965) came to a similar conclusion on the grounds of visual masking experiments.

Thus, there is evidence for channels tuned both to spatial frequency and to orientation. Such an interpretation is supported by

the finding that an observer's grating acuity is lowered by adaptation to a grating of identical orientation and bar width, but higher contrast (Blakemore & Campbell, 1969a). For the effect is decreased if either the orientation or the spatial period is altered relative to the adaptation grating (Pantle & Sekular, 1968b, Blakemore & Campbell, 1969a, b).

Now there are, in fact, neurones in the central nervous system of the cat which are selectively sensitive to both the orientation and the spatial frequency of a grating stimulus (Campbell et al., 1968, 1969a). But there are at least two difficulties in relating human psychophysical phenomena to cat single unit data. Firstly, it is by no means certain that the visual systems of cat and man are sufficiently similar to justify such conclusions; and secondly, psychophysical threshold data cannot be directly compared with single unit data recorded at supra-threshold levels. These difficulties led Blakemore & Campbell (1969a) and Campbell & Maffei (1970) to use VEPs as a linking technique.

Blakemore & Campbell (1969a) found that the previously-mentioned adaptation phenomenon, whereby the contrast threshold for detection of a low contrast grating was raised by previous inspection of a similar grating of high contrast, was mirrored in the VEP to alternation of the grating pattern. For the VEP was virtually abolished under the conditions for which the contrast level was roughly at threshold.

Campbell & Maffei (1970) recorded VEPs to the alternation,

at 8 Hz, of a sinusoidal grating. The relationship between the log. of contrast and the VEP amplitude was linear, and extrapolation to zero VEP amplitude accurately predicted the psychophysical contrast threshold, over a wide range of spatial frequencies. This result supports the validity of comparing the supra-threshold data from single units with the threshold data of psychophysics. It was also found that the slope of the regression line was remarkably constant. This could only be increased by simultaneously stimulating with more than one spatial frequency or orientation. The suggested explanation was that the magnitude of the VEP was related to the number of orientation-selective and spatial-frequency-selective channels activated.

One surprising characteristic of the VEPs recorded by Campbell & Maffei (1970) is that they did not depend on the area of retina stimulated. They state that there was no difference between the upper and lower half-field responses. This contrasts with the reports of polarity reversal between the VEPs to the upper and lower half-fields by Halliday & Michael (1970) who used checkerboard alternation and Jeffreys (1969) who used pattern-appearance. Even flash VEPs are sensitive to retinal area (Rietveld et al., 1965). Campbell & Maffei observed that the lack of independence of their VEPs on retinal locus was surprising in view of the strict topographical projection between retina and striate cortex observed by (e.g.) Cowey (1964). They suggested that the anomaly might be explained if the alternating grating stimulus preferentially activated complex and/or hypercomplex cells with large

receptive fields. That may be so, but it does not explain why the stimulus of Halliday & Michael (1970), which was also an alternating pattern, should have produced VEPs whose dependence on retinal locus was so much greater.

Another interesting correlation between VEPs and psychophysics was noted using, as above, an alternating grating as stimulus. It is well known that visual acuity is greater for vertical and horizontal targets than for obliquely orientated ones (reviewed in Taylor, 1963). Maffei & Campbell (1970) found that the VEP was greater for vertical or horizontal gratings than for oblique ones, although this effect did not manifest itself in the electroretinogram. Thus, the inequality presumably arose at some level central to the site of origin of the electroretinogram.

Interesting as the above results are, it must be added that none of the papers (Blakemore & Campbell, 1969a, b; Campbell & Maffei, 1970; Maffei & Campbell, 1970) state the number of subjects used. Since VEPs are notoriously variable between subjects, it would be premature to assume that the above results are universally valid.

1.5. Rationale for the present investigations.

It was emphasized in section 1.3. that both the form and the motion of a visual stimulus are important parameters for eliciting a response from single units in the brains of lower animals, and even man. This applies both in the cortex, and in certain lower brain centres such as the superior colliculi.

The importance of the form of the visual stimulus for activating cortical single units has led to the investigation of pattern-related VEPs in man, and these have been found to be in many ways a more useful object of study than VEPs to homogeneous flash, as was argued in section 1.1. In particular, pattern VEPs are less complex than flash VEPs, and are more easily related to the anatomy of the cortex.

It has been argued that stimulus motion is also likely to prove an important and interesting parameter in VEP research, since this too is an important parameter for the activation of cortical single units.

Moreover, psychophysical evidence has been cited in favour of the existence of motion-sensitive mechanisms in man; and despite some arguments to the contrary (e.g. Richards, 1971), it has been contended that the evidence, both behavioural and physiological, suggests that the visual cortex from which scalp-recorded VEPs apparently originate plays an important role in the detection, and indeed the perception, of motion. Thus one useful role for motion-evoked potentials is likely to be that of linking single unit data with the data of the psychophysics of motion-perception.

1.5.1. The choice of stimulus.

The evidence reviewed in this chapter suggests that the postulated motion-sensitive mechanisms are selectively sensitive to the direction of the motion. The stimulus for motion VEPs should therefore be such as is likely to produce a change in the activity of direction-selective mechanisms; and, ideally, in the activity of these alone. Furthermore, the responses of the direction-selective mechanisms should

be evoked specifically by virtue of their direction-selectivity. (This is not a truism; for example, mechanisms maximally sensitive to a stimulus moving in a particular direction might respond to some extent to a stationary flashing stimulus. Such responses, although evoked in direction-selective mechanisms, would not be genuine motion-evoked responses.)

Now the extent to which a stimulus meets such criteria is, in the last resort, an empirical matter, but the probable merits of various classes of stimulus can be evaluated on general theoretical considerations. For example, the sudden appearance at constant luminance of a moving pattern would be an unsuitable stimulus because it would be likely to evoke a response from contrast-sensitive mechanisms irrespective of whether they were direction-selective. A repetitively scanning spot, such as was used by Dawson, Perry & Childers (1968), would also be unsuitable, because it would probably activate direction-insensitive mechanisms sensitive to brightness and contrast as its image traversed the retina; and, even worse, the successive local responses would be delayed with respect to each other, causing more confusion in the resulting VEP.

The onset of motion of a stimulus line would also probably produce a change in the activity of other than direction-selective mechanisms, although the control experiments of MacKay & Rietveld (1968) indicate that in their experiments there was no significant off-response due to the stimulus line leaving the fovea.

The onset and offset of motion of a stimulus pattern might be expected to elicit very little response except from direction-selective mechanisms, but in fact, even with this stimulus, that is by no means certain to be the case. Firstly, it is known that the contrast threshold for detecting all but the slowest of moving targets is higher than that for the detection of similar stationary targets (van Nes, 1969); and for this reason, the onset and offset of target motion would be likely to produce a change in the activity of contrast-sensitive mechanisms. Secondly, a moving patterned stimulus would continually be exciting different contrast-sensitive mechanisms (which may or may not be direction-selective) as the pattern element moved into new receptive fields, but a stationary pattern would not produce such effects, except to the extent that these were caused by the small eye movements which occur during fixation. Thus, the onset and offset of motion would be likely to produce changes in the statistical pattern of activity of neural mechanisms, irrespective of whether these were direction selective, and the changes might contribute to the VEP.

Not so with motion-reversal. The only parameter to change during motion-reversal is the direction of motion. Both the effective contrast and the pattern of activity of direction-insensitive neural mechanisms will be the same before and after motion-reversal. (That would not be true for a pattern with a luminance profile which was asymmetrical with respect to the two directions of motion - for example, a grating with a sawtooth luminance profile. But for a symmetrical

pattern such as a checkerboard or square wave line raster, or for a random noise pattern, it is true.)

Even so, motion-reversal cannot be guaranteed to produce a VEP which is purely the response of direction-selective mechanisms. For at the moment of reversal there will be a very brief slowing down, which might result in the activation of contrast-sensitive mechanisms. Even instantaneous reversal might produce an increase in the effective contrast, and various other effects which could activate direction-insensitive mechanisms. Such possibilities are considered in detail in chapter 3.

Despite the fact that motion-reversal cannot be guaranteed to produce a purely motion-evoked response, it is probably less likely to elicit contributions from other sources than are any of the alternative stimuli. Also, it is known to produce fairly large VEPs, and there is tentative evidence (to be discussed in the next sub-section) that these are not purely the product of pattern-appearance sensitive mechanisms (MacKay & Rietveld, 1968; Rietveld & MacKay, 1969a, b). For these reasons, motion-reversal VEPs were chosen as the main object of investigation, although VEPs to motion-onset and offset were also investigated.

1.5.2. Existing data on the extent to which motion-reversal VEPs reflect the activity of direction-selective mechanisms.

Rietveld & MacKay (1969a, b) compared the VEPs to pattern motion-reversal and to pattern-appearance, as is briefly described in section 1.1.5. One purpose of these experiments was to investigate whether there were any differences between the mechanisms underlying the two kinds of VEP.

Investigating the above question is not logically equivalent to investigating the extent to which direction-selective mechanisms contribute to motion-reversal VEPs. For on the one hand it is possible that direction-selective mechanisms might contribute to both kinds of VEP; and on the other hand it is possible that direction-insensitive mechanisms which did not contribute to the pattern-appearance VEPs might nevertheless contribute to the motion-reversal VEPs. The latter possibility is unlikely, however; it is probable that any mechanisms contributing solely to the motion-reversal VEPs would be direction-selective.

Rietveld & MacKay (1969a, b) found that the two kinds of VEP had very similar waveforms, and approximately the same distribution over the scalp; but there were also three distinct differences between the two kinds of VEP, and these will be discussed in some detail below.

(i) Decreasing the contrast of the pattern diminished both the motion-reversal VEPs and the pattern-appearance VEPs; but it increased the latency of the main negative peak of the latter without affecting the latency of the corresponding peak in the former (Fig. 1.1.2a).

(ii) The VEPs to the reversal of motion of a checkerboard pattern included a negative double peak, in which the two components were differently affected by changes in check-size, but pattern-appearance VEPs included no such double peak (Fig. 1.1.2b). This was observed for several subjects (Rietveld & MacKay, personal communication).

(iii) The latency of the pattern-appearance VEPs varied somewhat over the scalp, whereas the latency of the motion-reversal VEPs did not seem to do so. But this result was obtained for only one subject

(Rietveld & MacKay, personal communication).

These differences were interpreted by Rietveld & MacKay (1969a) as tentative evidence that different mechanisms were involved in the two kinds of VEP. This evidence must, indeed, be regarded as very tentative for the following reasons.

Since the method of stimulation was different in the two cases, one would expect the two kinds of VEP to have different properties even if they did originate in the same mechanisms. It must be remembered that pattern-appearance VEPs comprise several different peaks, which depend differently on such parameters as appearance-duration and contrast (Jeffreys, 1970, 1971, and unpublished data); and the natural null hypothesis is that motion-reversal VEPs are similarly complex. It is thus quite conceivable, for example, that had Rietveld & MacKay used a different appearance-duration (e.g. 5 msecs instead of 500 msecs) the pattern-appearance VEPs would have depended on contrast, check-size and scalp location in much more nearly the same way that motion-reversal VEPs do. It should be noted in this connection that changes in the apparent latencies of VEPs are not necessarily caused by changes in the response latencies of the underlying mechanisms; they may be caused by changes in the relative amplitudes of separate components of constant latency. So the different effects of contrast level on the latencies of the two kinds of VEP may have been caused by differences in the relative amplitudes of the underlying components of the two kinds of VEP; and, as stated above, the relative amplitudes of the pattern-appearance VEP components are dependent on the duration of pattern-appearance.

Moreover, the visual field sizes used were very different for the two kinds of stimulus; 17° for motion-reversal and $5\frac{1}{2}^{\circ}$ for pattern-appearance (Rietveld & MacKay, personal communication). These differences in field size provide another possible explanation for the differences between the two kinds of VEP.

Finally, there is evidence that the variation of the latency of the main peak of pattern-appearance VEPs over the scalp, reported by Rietveld & MacKay (1969a) does not reveal any fundamental property of the underlying mechanisms. For Jeffreys (personal communication) has found that although the apparent latencies of whole-field pattern-appearance VEPs do sometimes vary over the scalp, this does not occur for either upper or lower half-field stimulation. The changes in latency over the scalp of the whole-field VEPs appear to be due to the differences between the distributions and waveforms of the constituent half-field VEPs.

Despite these criticisms, it remains true that the differences between the two kinds of VEP studied by Rietveld & MacKay are, as they claim, suggestive of differences between the underlying mechanisms. But they do not claim to have shown, even tentatively, that pattern-appearance VEP mechanisms do not contribute at all to the motion-reversal VEPs.

To summarise, the existing data (prior to this thesis) tentatively suggested that the VEPs to motion-reversal might not be purely the response of the mechanisms underlying pattern-appearance VEPs, which in turn suggested that direction-selective mechanisms might be involved. The extent of such involvement, however, was not known.

Hence, the first question which required to be tackled in this research project was whether the motion-reversal VEPs genuinely reflect the activity of direction-selective mechanisms; and, if so, to what extent.

CHAPTER 2

Methods

2.1. Recording procedure

Forty nine subjects were used in a total of 102 experimental sessions. Almost all were between 17 and 30 years old, but two (J.M. and M.M.) were about 9 or 10 years old. Initially, both monopolar and bipolar recordings were used, to determine the more suitable recording method. Monopolar recording, using several electrodes, was chosen, because the monopolar responses were less complex and less variable between subjects than the bipolar responses (see Goff, Matsumiya, Allison & Goff, 1969).

Standard non-polarizable silver-silver chloride electrodes were used. They were attached to the scalp, and to both ear lobes or mastoids, with collodion, and conducting electrode jelly was injected into the electrodes so that the resistance between electrodes was stable and below 10 kilohms; there was very little electrical interference for electrode resistances of this order.

The right ear electrode was used as reference, and the left ear was earthed. The location of the scalp electrodes varied according to the experiment, but there were normally between four and ten including one on the inion and three more anterior to this on the midline at 3.5 cm intervals. These four electrodes normally covered the area of scalp where the VEP was largest. For EOG recording, the electrodes were attached by means of double-sided sellotape near the outer canthus of each eye.

The recording arrangement is shown in Fig. 2.1.1. The Digitimer (Devices Ltd.) synchronously triggered the stimulus and the Computer of Averaged Transients (CAT 400B). A Beckmann sixteen channel EEG machine was used. The bandwidth of the EEG amplifiers was set at 0.5 - 50 HZ, and the CAT sampling rate for each of its channels was never less than 200/sec. The maximum number of CAT channels was four, but this did not limit the number of electrodes as the raw EEG was also recorded on a 14 channel frequency modulated tape recorder. The CAT trigger-pulse was recorded on one channel of this. The averaged output from the CAT was recorded using an X-Y plotter. The whole recording system was calibrated using both positive and negative calibration pulses, from a pulse-generating facility of the EEG machine. Tape recording was carried out at 1.75 i.p.s., but replay at 7.5 i.p.s. Correct reproduction of the averaged calibration pulses indicated that the tape-recorder was functioning correctly. Aperiodic triggering was provided by means of a tape loop with eleven transparent notches cut at irregular intervals, which triggered a phototransistor unit. In the most commonly used arrangement the successive time gaps were: 460, 520, 480, 495, 505, 505, 465, 525, 445, 540, 495 msecs. Periodic triggering was provided by the digitimer's internal trigger.

The subject sat in a comfortable chair of adjustable height, in a soundproof room screened from electrical interference. The lighting was always low, and the subject was not aware of it during runs. He was asked to find a relaxed sitting position, to avoid moving during runs, and to fixate on the small, faintly illuminated red cross provided

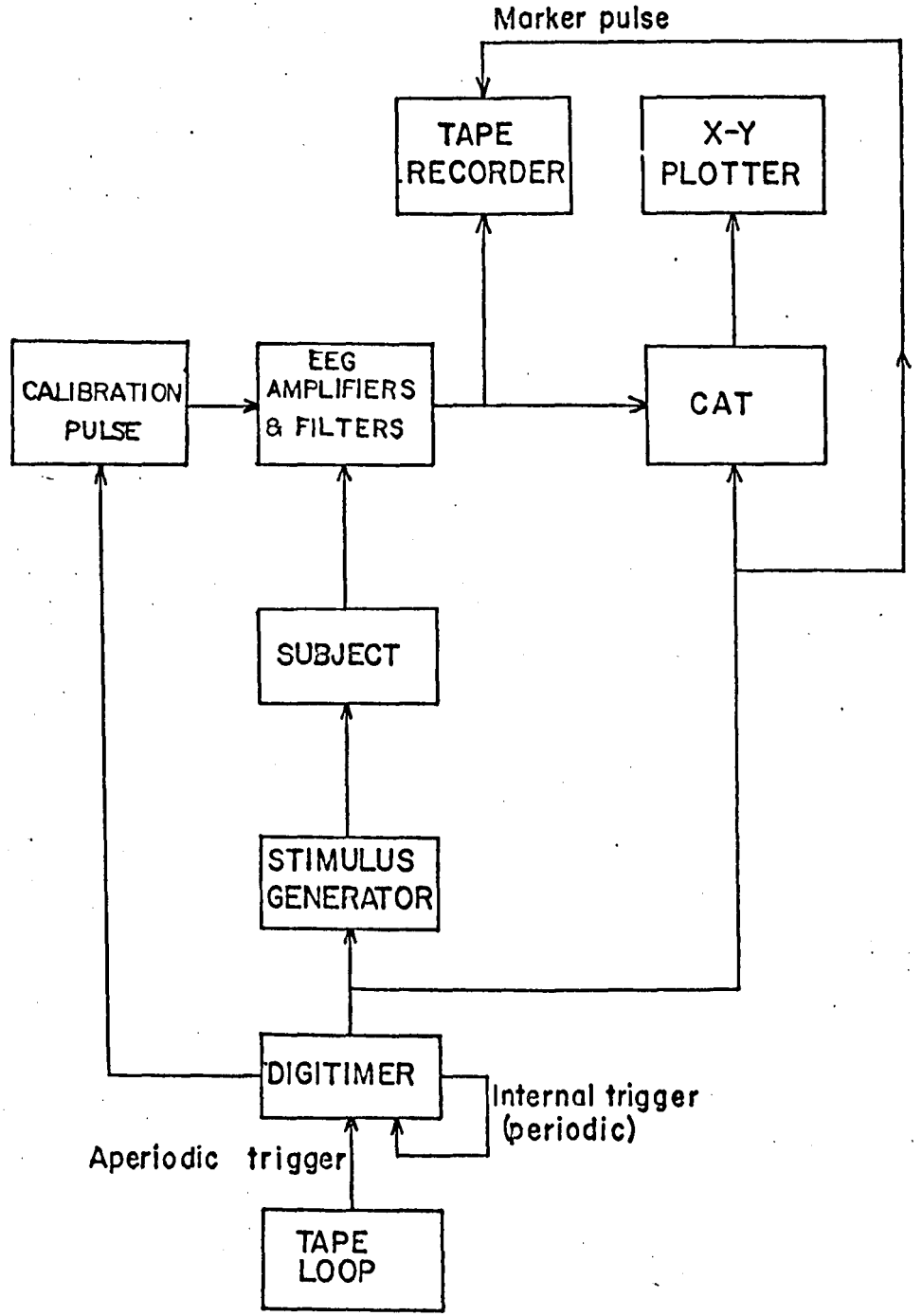


Fig.2.1.1. Block diagram of the experimental system.

for that purpose in the centre of the visual field. Every care was taken to ensure that the subject was fully relaxed, partly because there is evidence (Bickford, Jacobson & Cody, 1964) that auditory evoked potentials to clicks and VEPs to flashes can be seriously contaminated with myogenic components if the subject is not properly relaxed; although the bulk of evidence suggests that such contamination is rarely serious in visual evoked potentials (Katzman, 1964). It is very unlikely that myogenic artifacts were present in the VEPs reported in this thesis, as the VEPs were always localised over the occipital and occipito-parietal scalp, with characteristic changes in spatial distribution for stimulation of different areas of the retina. Myogenic components would not exhibit such properties.

Experiments lasted about one and a half hours. This included about thirty runs lasting about eighty seconds each, interspersed with gaps during which the subject rested while the results were being plotted out.

Every stimulus was repeated at least once. If a stimulus variable X was given successive values X_1, X_2 - - - X_{n-1}, X_n, this series would then be repeated in the reverse order X_n, X_{n-1}, - - - X_2, X_1, to eliminate possible effects of gradual fatigue etc. The earliest runs were often repeated at the end of the experiment, but there was normally no significant change in the response during the experiment. On rare occasions, however, a subject did become so tired that the VEPs were affected, but in such cases the VEPs also became very variable and the experiment was abruptly ended.

2.2. Visual stimuli.

Two main kinds of visual stimulator were used. One, which will be referred to as 'the mirror system' involved the movement of a pattern, back-projected on a screen via a mirror which was driven to provide the movement. The second will be referred to as 'the tachistoscopic system'. This involved optically switching from one tachistoscope channel to another, so that one and only one channel was visible at a time. Each channel contained a blank field, a stationary pattern or a moving pattern. The pattern was normally 'visual noise' (Fig. 2.2.1), (see MacKay, 1961b), of the same grain size in each system (the size of the noise in the figure, viewed from 48 cm).

2.2.1. Mirror system.

With this system, a slide projector was used to back-project a pattern onto a screen via a moving mirror. The subject viewed the screen through an aperture, cut in black cardboard, in the plane of the screen. Unless otherwise stated, the lower half-field (4° radius) was used. Luminance was varied by means of an aperture in front of the projection lens and by neutral density filters. The subject fixated on a small red cross in most experiments, but on a small red spot in the earliest ones.

The arrangement for driving the mirror is shown in Fig. 2.2.2. The Pulse Inverters were simple grounded emitter amplifiers, and were used because the Tektronix 161s (pulse generators) required a positive trigger pulse. The Tektronix 161s provided a pulse whose amplitude, duration and polarity could be independently controlled.

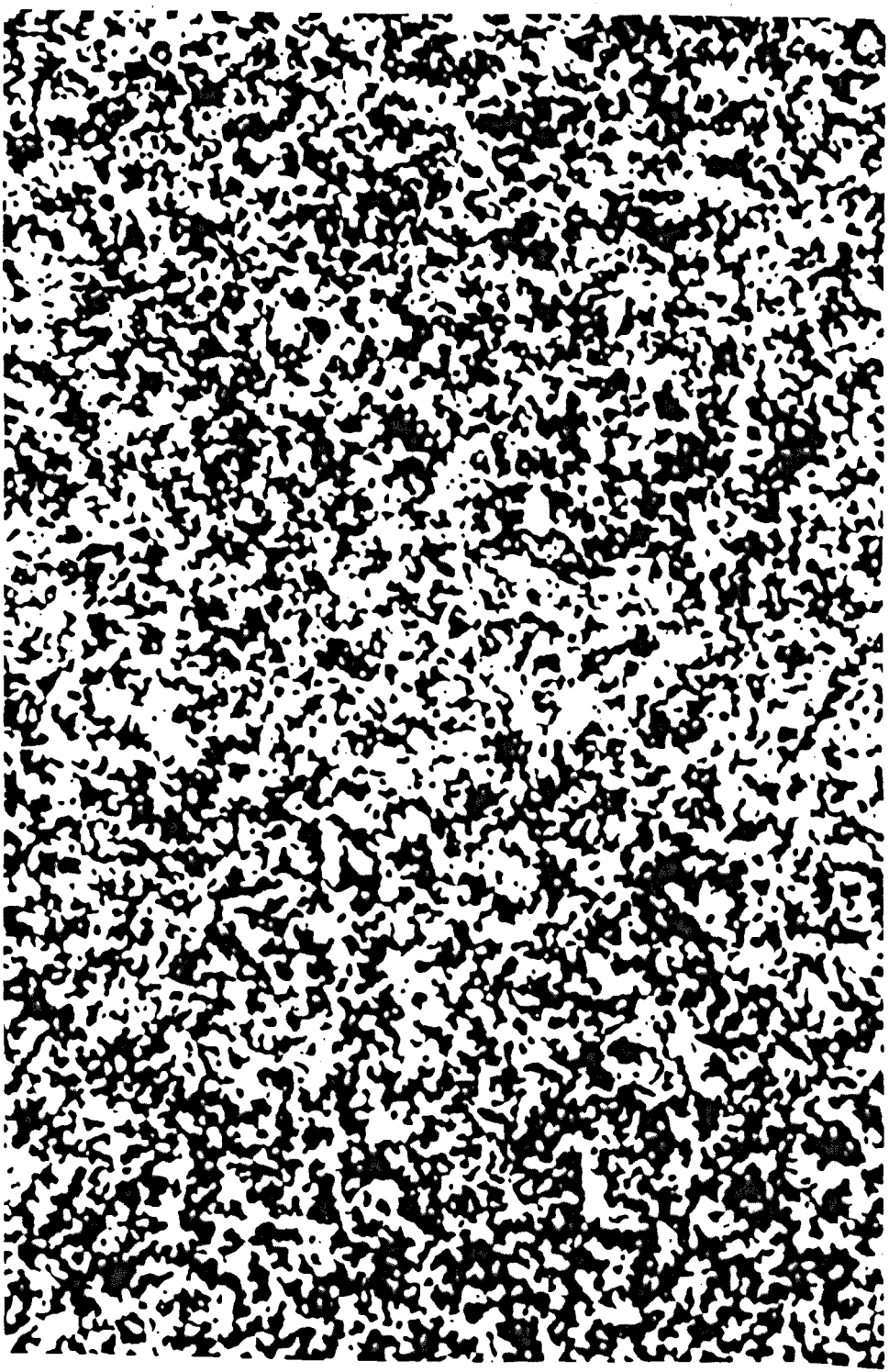


Fig.2.2.1. Visual Noise.

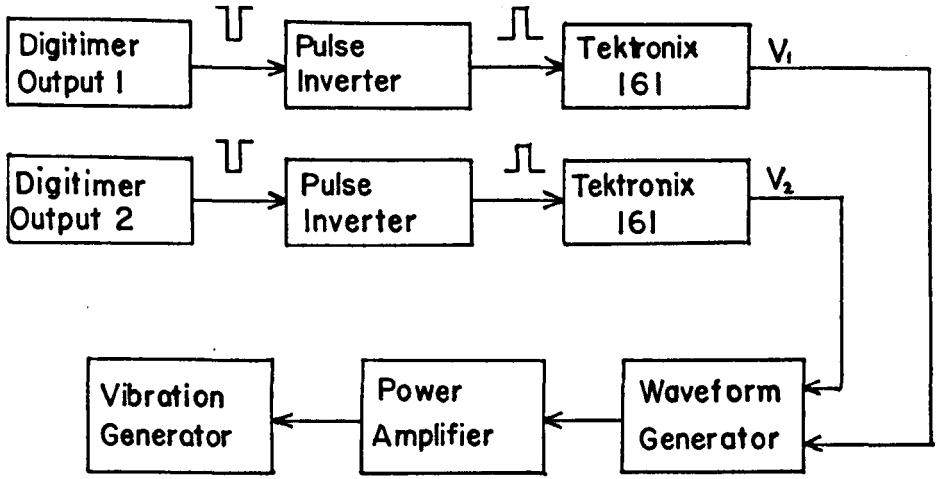


Fig.2.2.2. Block diagram of the mirror control system.

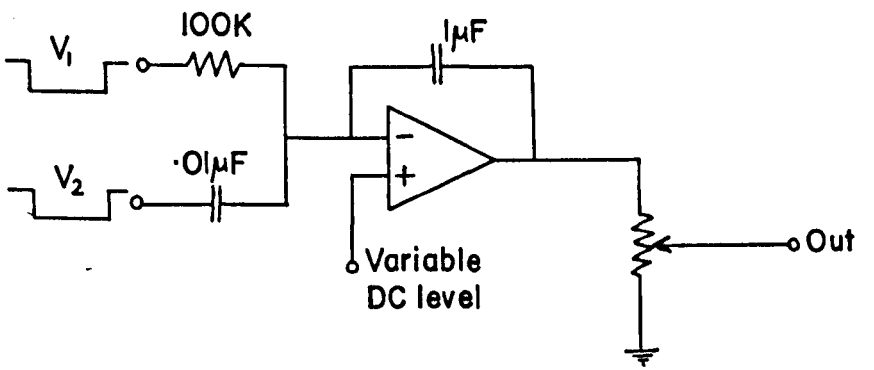


Fig.2.2.3. Waveform Generator.

The waveform generator (Fig. 2.2.3) integrated a square-wave at input 1, producing a triangular waveform, but other variations (Fig. 2.2.4) were made possible by additional use of input 2 and the property of amplifier saturation at the supply voltage (± 9v). Bottom-saturated waveforms were normally used to prevent DC drift.

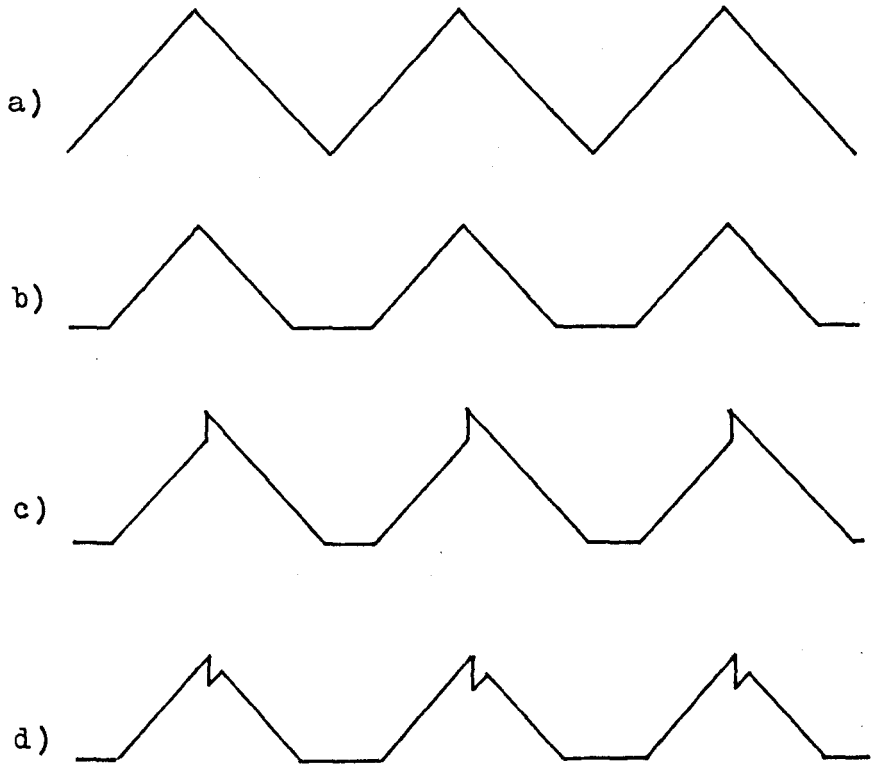
The input resistance of the Vibration Generator was about 3 ohms, so a power amplifier with output impedance of that order was constructed from a circuit (Fig. 2.2.5) described by Van der Mark (Schipperheyn, 1965) and modified by R.F. Cartwright. The power transistors (OC 28s) at the output were a matched pair, and were mounted on a heat sink. The variable resistor controlled the DC level.

The 'Vibration Generator' was essentially a linear motor with a wide bandwidth frequency response between DC and about 1 kHz, when not mechanically loaded. Fig. 2.2.6 shows how the Vibration Generator was used to rotate the front-silvered mirror about a vertical axis through its reflecting surface. The system was made as small and light as possible in order to minimise the moment of inertia and so obtain a good frequency response. This was important for producing a rapid turn-round time in motion-reversal. For the same reason, the ball-bearings and pin-hinges were kept well oiled.

The system normally produced horizontal motion, but the direction of motion could be varied by means of a Dove prism.

The Electromechanical response of the system.

Fig. 2.2.7 shows the frequency response of the system, from the input to the power amplifier to the motion produced on the screen.



a) Triangular waveform. V_1 is a regular square-wave; $V_2=0$.
b) Bottom-limited triangular waveform. Inputs as for a).
c) Bottom-limited triangular waveform plus step. V_1 is a regular square-wave. $V_2=-kV_1$.
d) As c), except $V_2(t) = kV_1(t+T)$, where T is about one twentieth of the period.

Fig.2.2.4. Waveforms that could be produced with the Waveform Generator.

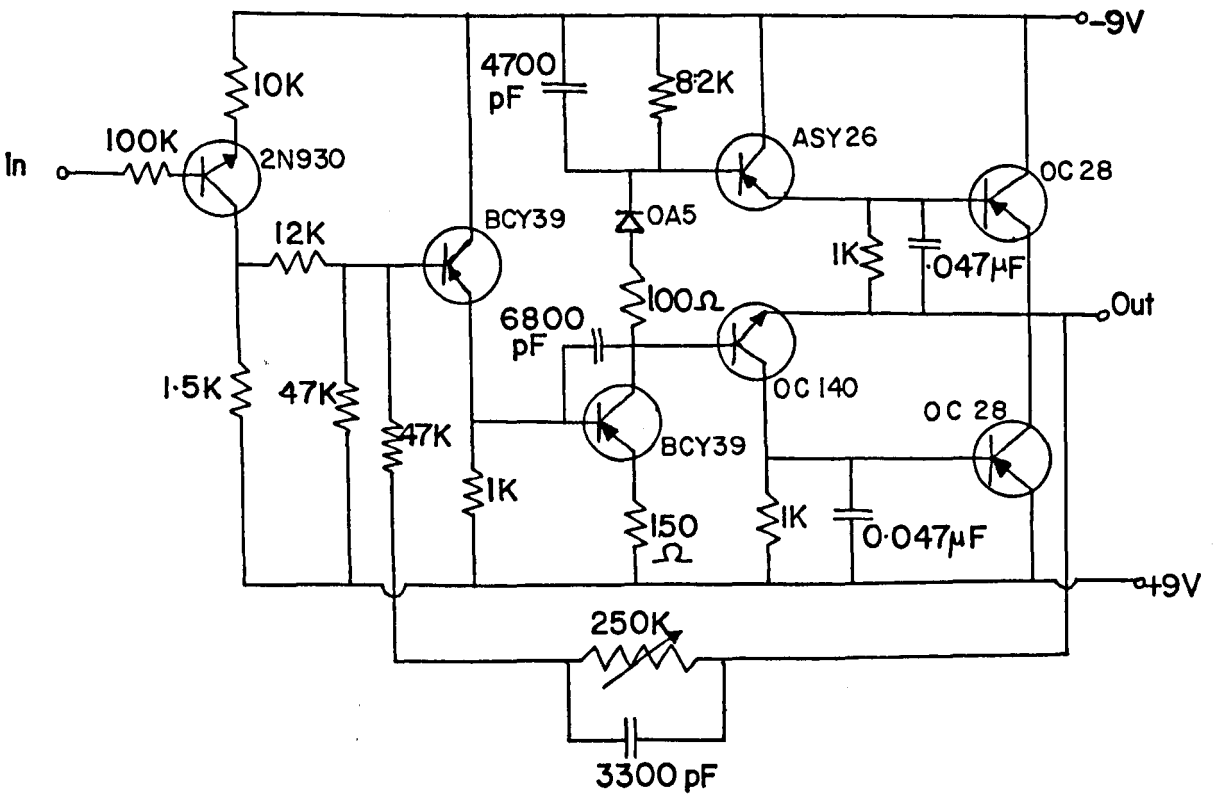
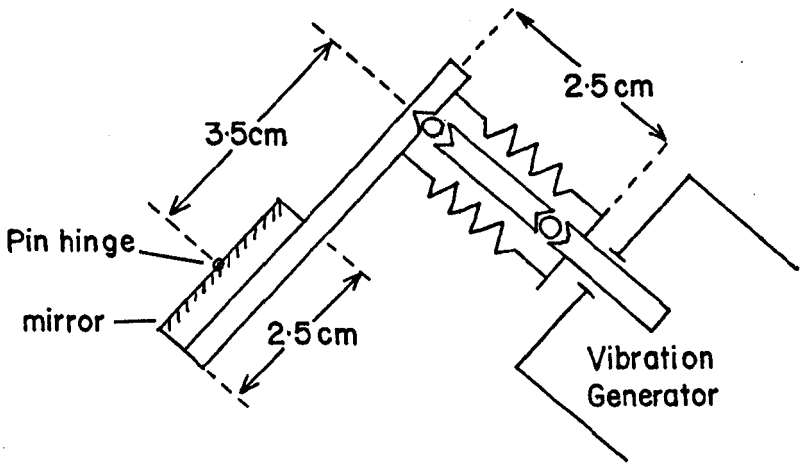
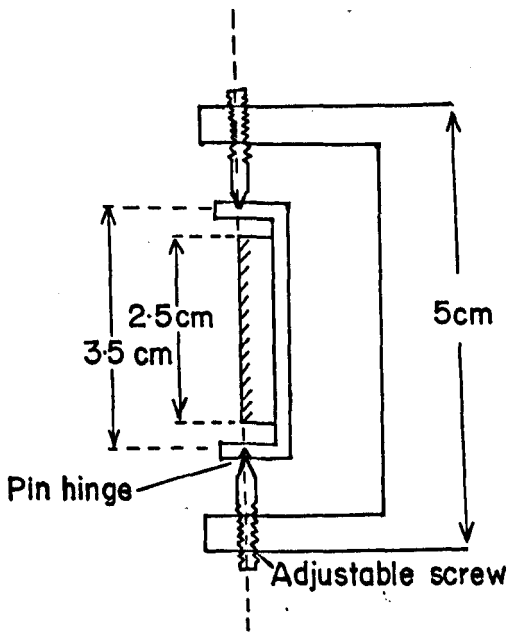


Fig.2.2.5. Power Amplifier.



a) Plan View.



b) Side View of Hinge Arrangement.

Fig.2.2.6. Mechanical coupling between vibration generator and mirror.

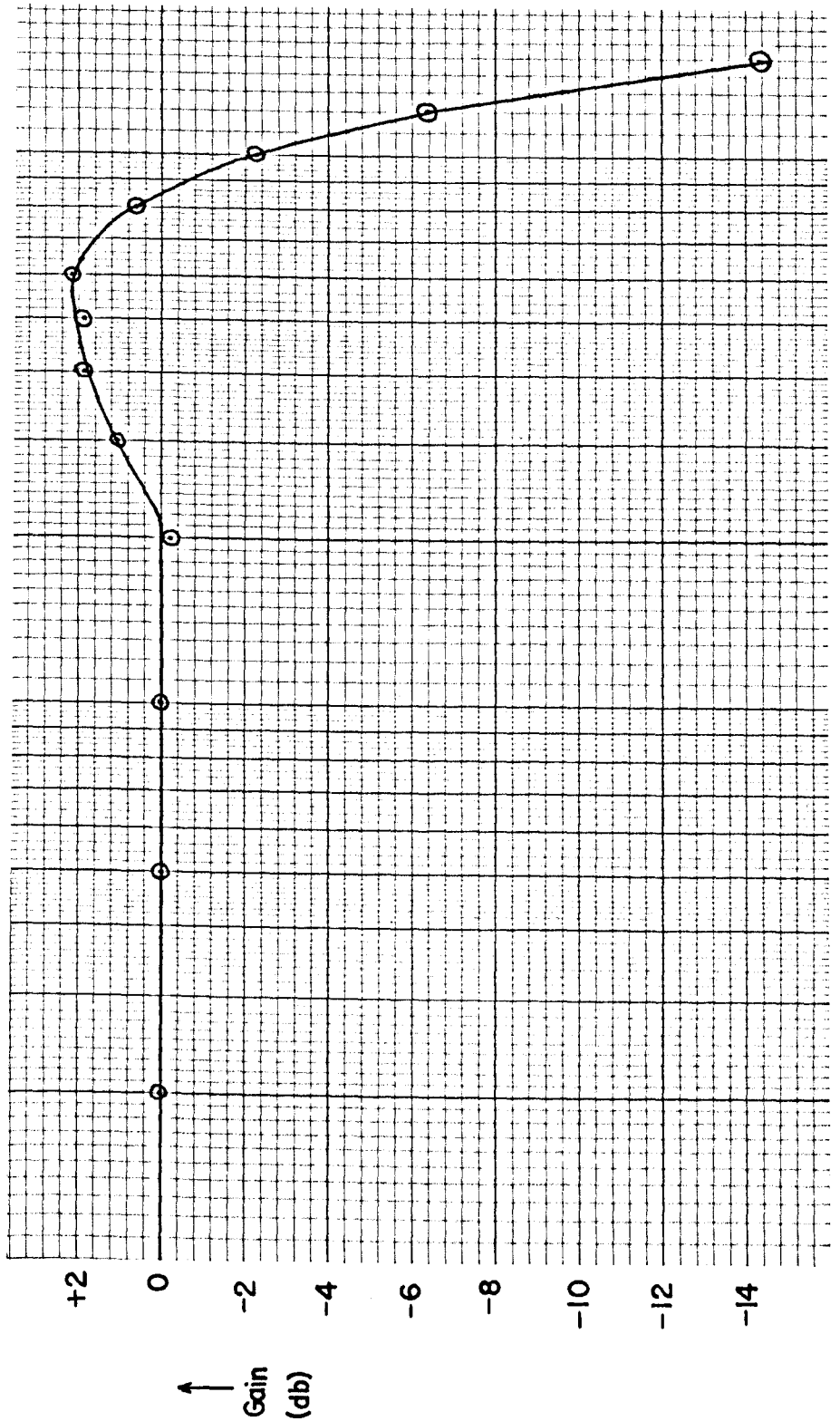


Fig. 2.27. Amplitude-frequency characteristics of the mirror system.

The - 3db cut-off frequency is greater than 100 Hz.

It is possible on the basis of this to make a rough estimate of the time taken for velocity-reversal, by comparison with a one-stage RC filter of the same cut-off frequency (f_c). If f_c = 100 Hz, time constant RC = $1/2\pi f_c$ = $^1/(2\pi \times 100)$ = 1.6×10^{-3} secs. Hence the time function at reversal after filtering,

Velocity $V(t) = V_{max}(1 - 2e^{-t/RC})$ (See Appendix 1)

where V_{max} is the final velocity (so initial velocity = $-V_{max}$)

Hence after 5 msecs, $V = V_{max}(1 - 2e^{-3.1})$

$= V_{max}(1 - 0.09)$

$= 0.91\ V_{max}$

So in this case reversal is virtually complete after 5 msecs.

For a filter with perfect cut-off at f_c = 100 Hz, the turn-round time = $\frac{1}{2f_c}$ = 5 msecs, the same result.

It can thus be assumed that motion-reversal is virtually complete within 5 msecs.

This was confirmed by recording directly the time function of motion at reversal. A black-white edge was projected through the system, and this was viewed through a rectangular aperture by a photomultiplier. The mains-powered projector lamp was replaced by DC-driven glow tubes so the light flux at the photomultiplier contained no variation due to mains oscillation and was therefore proportional to the position of the edge. The relationship between the light flux received by the photo-multiplier and its output was linear. This output voltage was therefore proportional to the position of the edge. It was observed on an

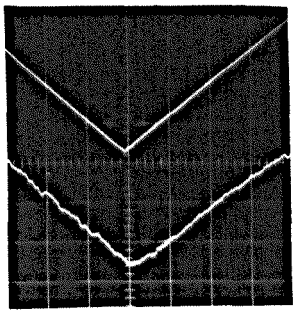
oscilloscope screen, and Fig. 2.2.8 shows oscilloscope traces indicating the movements produced by various inputs. It can be seen that the time for complete reversal of motion was about 5 msecs, as predicted. There is no indication of overshoot, and a superimposed step in the input voltage is quite faithfully reproduced in the output.

In some experiments a variable time-constant low-pass filter was added between the Waveform Generator and the Power Amplifier. This was constructed according to the circuit in Fig. 2.2.9. The emitter-follower at the input was necessary so that changes in the output impedance of the Waveform Generator would not affect the time constant of the filter. Time-constant values were calculated (39 k.ohms x C) ignoring the output impedance of the emitter-follower. The frequency characteristics of the filter were recorded, and these confirmed the validity of the assumption. The time-constant values were:

1.9, 2.8, 4.1, 6.4, 8.8, 12, 18 msecs.

Wave-shaping of the mirror-control signal was sometimes used to decrease the turn-round time at reversal. On the assumption that the mirror system behaves approximately as a simple RC low-pass filter, its transfer function is

$F(s) = \frac{1}{1 + Ts}$, where T is the time-constant (approx. 1.6 msecs). If the time-differential of the input is added, $F(s) = \frac{1 + as}{1 + Ts}$. Hence, if $a = T$, $F(s) = 1$. This was achieved by adding a resistor in series with the feedback capacitor in the Waveform Generator (Fig. 2.2.10). Now $T = 1.6$ msecs, so $a = RC_2 = 1.6$ msecs, i.e. $R_2 = 1.6$ k.ohms. So the turn-round time should be decreased considerably by adding a 1.6 k.ohm



a) Motion-reversal takes place within 5msecs (one square represents 20msecs).

b) A superimposed step in the input voltage - time waveform is quite faithfully reproduced in the resulting stimulus motion.

Fig.2.2.8. The stimulus movements (lower trace) produced by two different inputs (upper trace) to the mirror system.

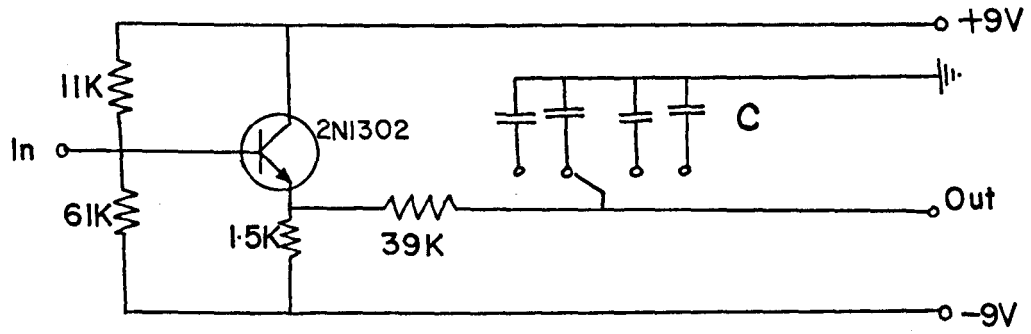
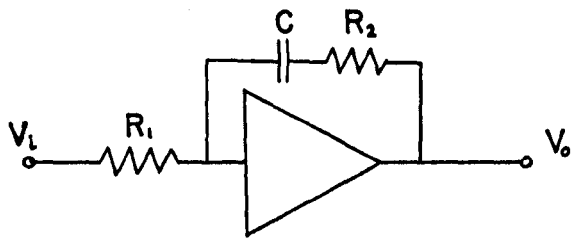


Fig.2.2.9. Low-pass filter with variable time constant.



$$\frac{V_o}{V_i} = \frac{-1/sC + R_2}{R_1} = \frac{1+sCR_2}{sCR_1}$$

Fig.2.2.10 Wave-shaping circuit.

resistor as described above.

The vibration-generator responded non-linearly for input voltages greater than 3V, so this value was never exceeded in experiments.

Production of continuous unidirectional movement.

The mirror could not, of course, produce continuous movement in one direction. This was achieved by means of a large (10.5 cm radius) transparent disc of visual noise (see Fig. 2.2.1) mounted on the geared-down shaft of a servo-motor so that its outer region fell in the focal plane of a projector. Rotation of the disc caused almost linear vertical motion on the screen, which could, if desired, be converted into horizontal movement by means of a Dove prism. The servo-motor driving the disc could be set at a steady angular velocity by setting the gains of its own control system, and a superimposed variable velocity could be added by means of external control signals.

In some experiments concerned with adaptation, a steady velocity was produced for a limited period (e.g. 20 secs) by means of the projector arrangement, and then suddenly changed to a different velocity while at the same moment the mirror system was set in motion with a triangular waveform, for another time interval (e.g. 5 secs). This arrangement utilised gating facilities provided with the digitimer (Fig. 2.2.11).

2.2.2. Tachistoscopic system.

The arrangement for this is shown in Fig. 2.2.12. Fields 1 and 4 contained rotating transparent discs upon which photographic

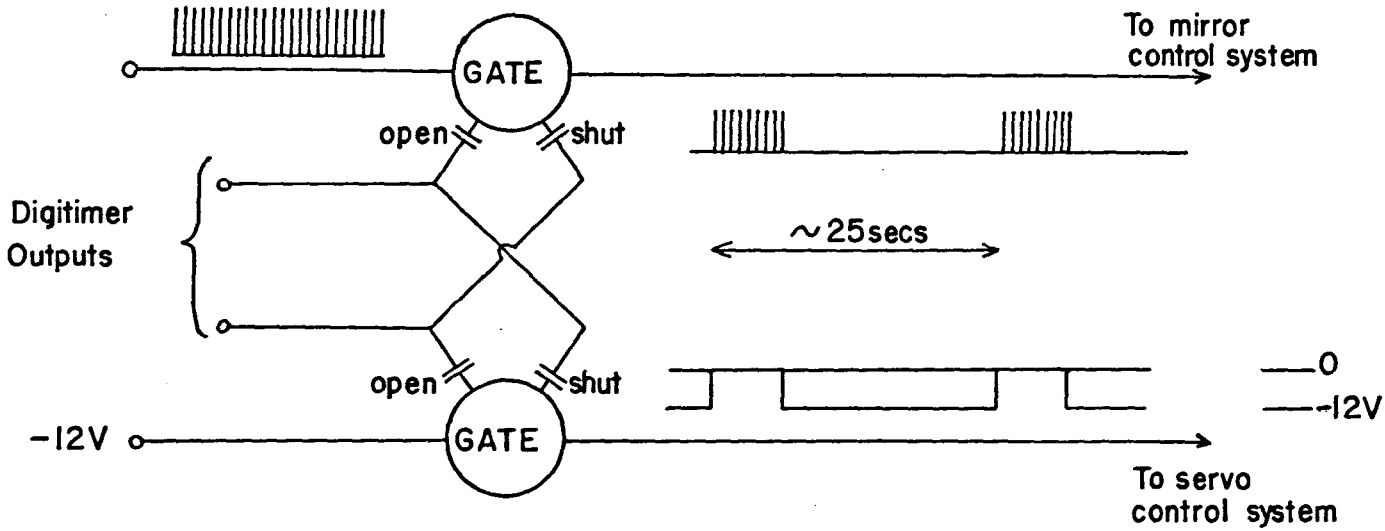


Fig.2.2.11. The arrangement for alternately gating the inputs to the servo and the mirror control systems.

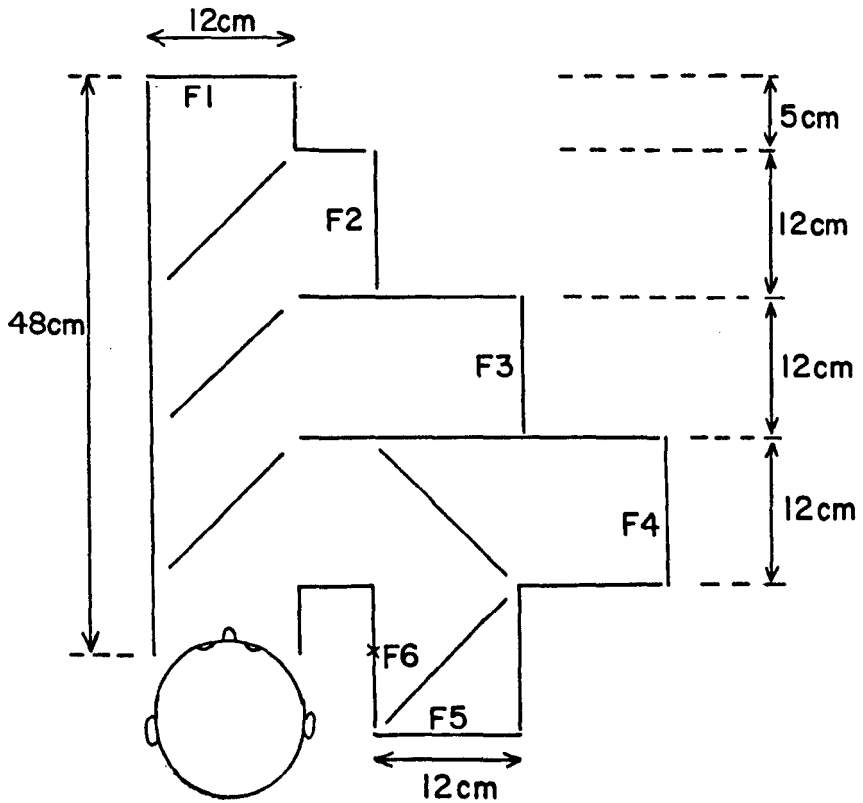


Fig.2.2.12. Basic layout of the tachistoscope. Field F6 contains the fixation cross. The diagonal lines represent half-silvered mirrors.

transparencies of visual noise were mounted. Fields 2 and 3 were used for blank or stationary pattern presentation and field 5 for providing steady illumination of the surround field. A small red fixation cross was placed in field 6. Each field was delimited by a cardboard aperture. Fine adjustments of the positions of the half-silvered mirrors brought each field and the fixation cross into the same plane (judging by absence of parallax) and visual position. The field size and viewing distance were the same as for the mirror system.

The walls, floor and roof of the tachistoscope were made of wood, and all inside surfaces were painted matt black. Secondary reflections were partly eliminated using black cardboard masks.

Fig. 2.2.13 shows the method of mounting the discs. This method made it possible to adjust the direction of seen motion to any angle, by rotating the disc and its mountings about an axis through the centre of the aperture in that field. Each motor operated at voltages between 3 and 12V, and included a '6 speed' gear-box (ratios 3:1, 6:1, 12:1, 16:1, 32:1, 60:1). The output shaft fed a second 50:1 gear-box, and the disc was mounted on the output shaft of this. This system permitte disc speeds providing linear stimulus motion between 1 and 30° visual angle/sec.

Each field was back-illuminated by two gas discharge tubes behind a white perspex diffusing screen. For most of the experiments tubes with a special rapid-decay coating were used. The tubes, which gave a bluish-white light, had emission rise and fall times of 0.5 msec

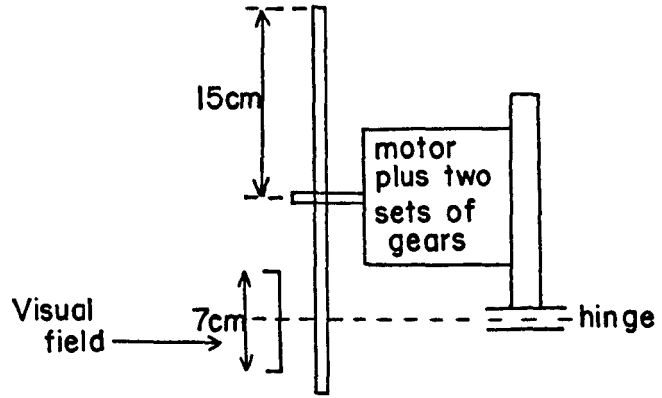
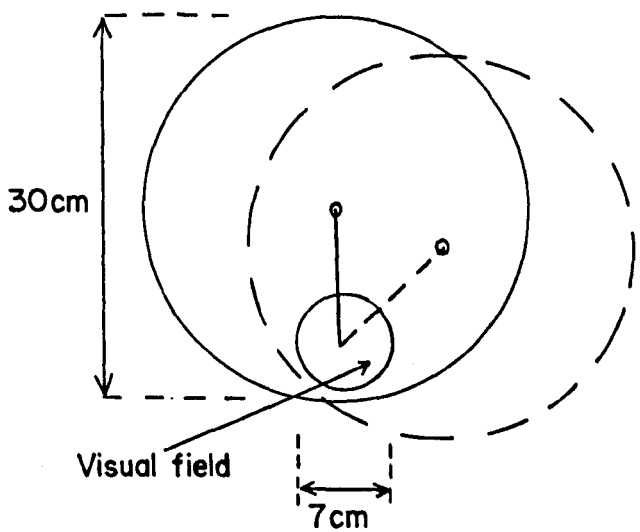


Fig.2.2.13 a) Side view of disc-mounting



b) End view of disc mounting. The visual field is seen through the disc. The disc is shown in two positions corresponding to horizontal and diagonal motion. (The dotted disc causes the diagonal motion to be seen).

(measured using a photomultiplier). In a few experiments tubes with 'daylight' coating were used, and these had 1.5 msec rise and fall times. The evoked responses are very similar for either kind of tube (D.A. Jeffreys, personal communication).

The circuit diagram for driving each pair of tubes is shown in Fig. 2.2.14. As the figure shows, the square-wave voltages required were produced by triggering bistable circuits (Fig. 2.2.15) with pulses from the Digitimer, delayed to switch on the bistable for the desired time interval. The bistable switched the high voltage (MJE 340) transistor fully on or fully off and this drove the gas discharge tubes. The 500 ohm potentiometer facilitated minor adjustments in brightness.

Firing of the tubes was facilitated by wrapping round each tube a wire, live at+150V but insulated from the tube.

2.3. Preliminary control experiments.

The averaged waveform recorded may include components from sources other than brain activity induced by the visual stimulus. These are considered below.

2.3.1. Instrumental artifacts and non-visual sensory artifacts.

Such artifacts were shown not to be present by covering up the visual stimulus. There was then no response. This control was carried out only occasionally, but it is certain that such artifacts would have been detected in any experiment, had they occurred, as there were always some control runs and stimulus conditions for which the response was very small.

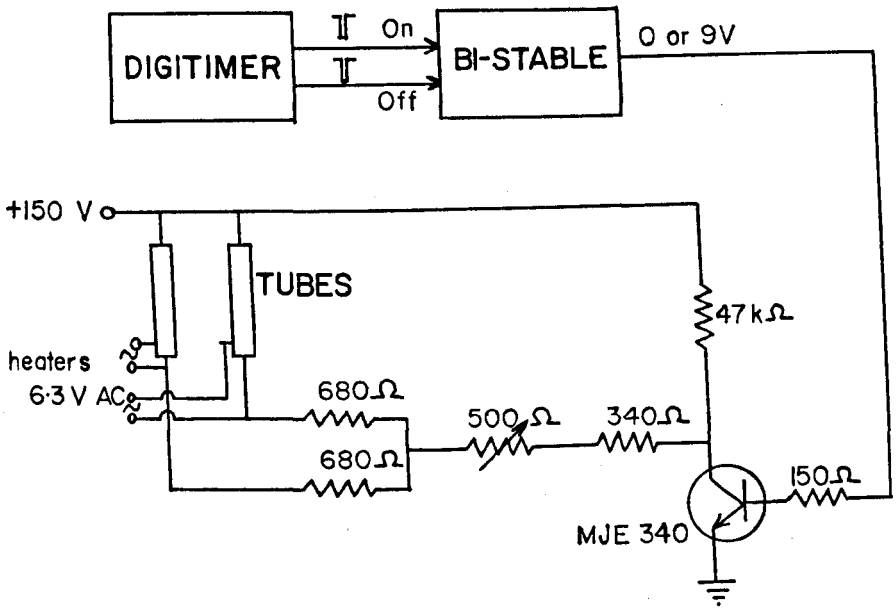


Fig.2.2.14. Driving circuit for the discharge tubes.

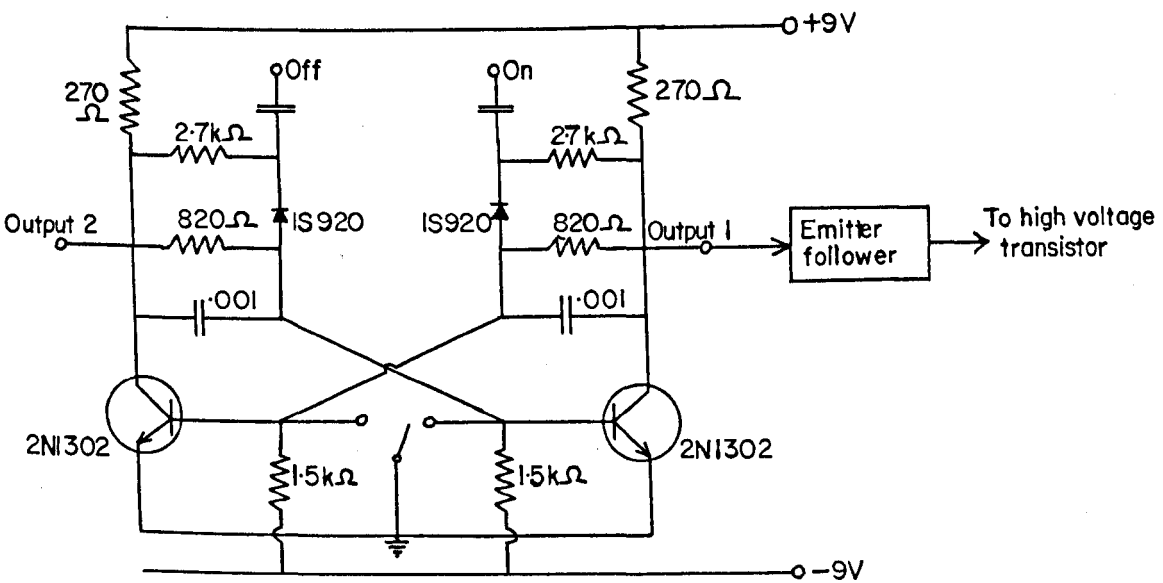


Fig.2.2.15. Bi-stable circuit.

2.3.2. Distraction due to the noise of the gears.

The gears through which the tachistoscope discs were driven made a certain amount of noise. This noise was not synchronised with the visual stimulus, but it might conceivably have affected the VEPs indirectly (e.g. through loss of attention to the stimulus). This was shown to be unlikely, however, because the VEPs to mirror-produced motion-reversal were quite unaffected by the noise of the tachistoscope discs.

2.3.3. Flash artifact.

The tachistoscope was always adjusted so that there was no subjective brightness change at switching, and in some experiments this was confirmed objectively using a photomultiplier. This was important to avoid contamination by brightness-change VEPs. Brightness-change VEPs are produced independently from pattern-appearance VEPs (Jeffreys, 1968a).

If the pattern was removed and the brightness readjusted to allow for removal of the pattern, the blank-to-blank VEP was usually of negligible amplitude (Fig. 2.3.1a). On two occasions, however, a rather large blank-to-blank VEP was produced, probably because the brightnesses were incorrectly adjusted. One of these cases is shown in Fig. 2.3.1b, and it can be seen that even in this case, which is about the worst I recorded, the blank-to-blank VEP is small compared with the pattern-appearance VEP. Fortunately the blank-to-blank artifactual VEPs were largest well anterior to the electrode (2) at which the pattern-appearance VEP was largest.

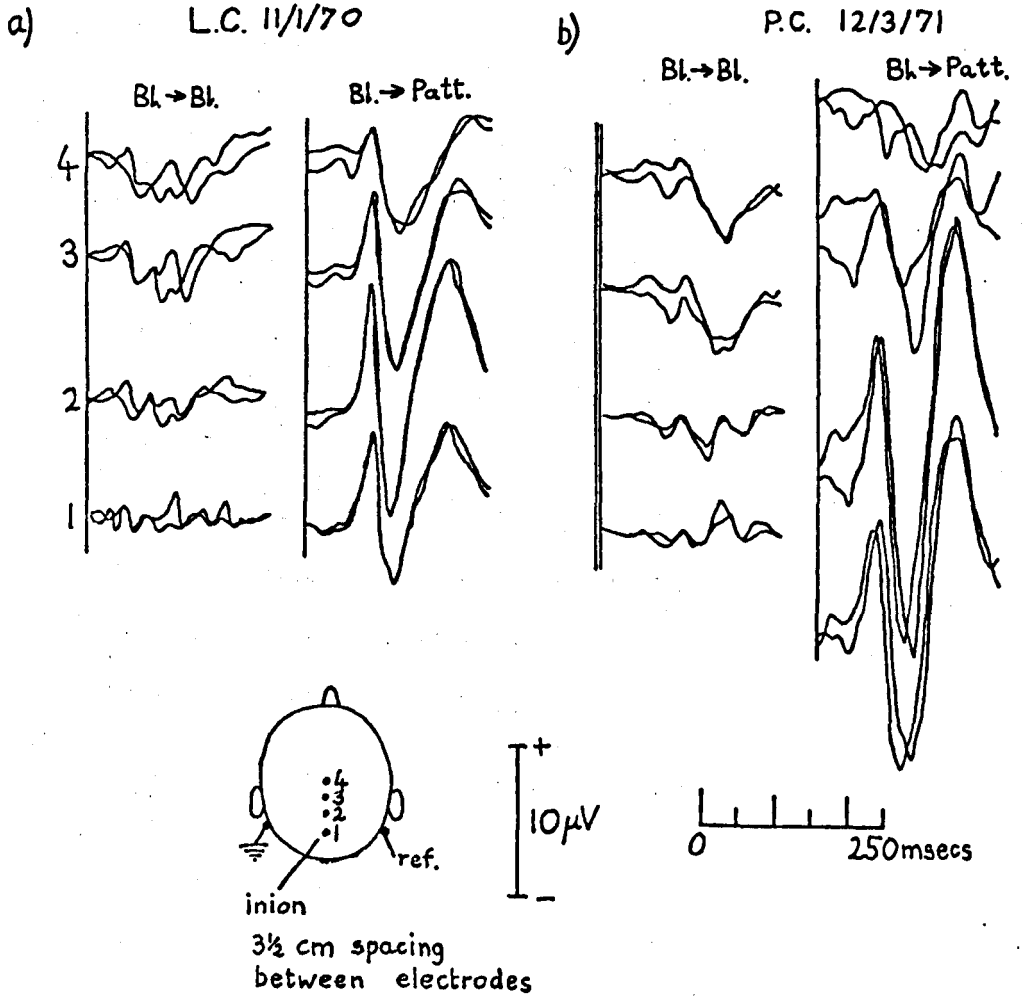


Fig.2.3.1 Blank-to-blank VEP compared with pattern -appearance VEP.

a) A typical subject.

b) A subject who gave a large blank-to-blank VEP.

Also, it should be noted that in many cases two VEPs were being compared, each of which would have contained an equal contribution from brightness-change artifact (e.g. the comparison of VEPs to stationary and to moving patterns).

2.3.4. Was the reference electrode neutral?

Halliday & Michael (1970) compared checkerboard-reversal VEPs for three different positions of the reference electrode: mid-frontal, mid-cervical and linked ear-lobes. They found that 'the responses were not entirely unaltered by a change of electrode', so clearly at least some of their reference electrodes cannot have been completely neutral. In a more recent paper (Michael & Halliday, 1971), they emphasize that, for upper half-field stimulation, the difference between the two-ear and the mid-frontal references is several microvolts, and they suggest that it is primarily activity at the ears which is responsible. Other investigators, using flash as the visual stimulus, have reached contradictory opinions as to whether the ear-lobes are neutral (Goff, Matsumiya, Allison & Goff, 1968; Lehtonen & Koivikko, 1971).

In the present series of experiments, the electrical activity at the reference electrode was investigated in three subjects by recording the averaged response between the chin and the right ear mastoid. (The latter was the usual reference electrode position although sometimes the ear-lobe was used.) Movement onset, offset and reversal did not give measurable chin-mastoid responses, but pattern-appearance did sometimes produce quite a large chin-mastoid response, especially for 40 msec presentation in the lower half-field (Fig. 2.3.2).

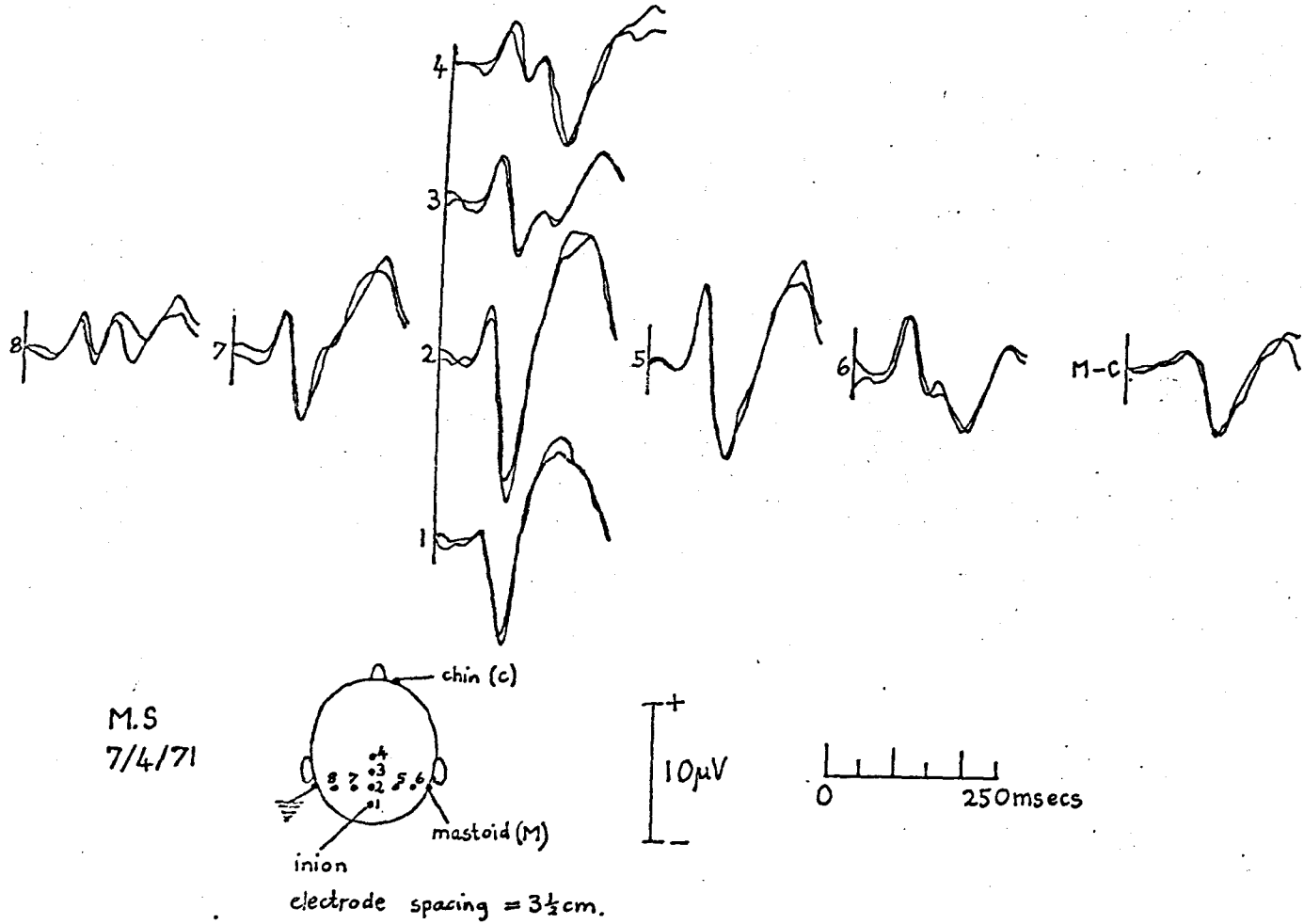


Fig. 2.3.2. The response at the right ear mastoid (M) relative to the chin (C) is compared with the monopolar recordings from eight scalp electrodes, using M as reference. The stimulus was 40msec pattern-appearance, lower half-field. For this subject, the M-C response was by no means negligible compared with the momopolar recordings.

Moreover, the smallness of the chin-mastoid responses for most of the stimuli used should not be taken to guarantee that the ear reference is neutral, because recent evidence suggests that there may have been substantial but similar activity at the two reference positions (Michael & Halliday, 1971).

As Michael & Halliday point out, activity at the reference electrode can be seriously misleading in an attempt to infer the location of VEP sources from the distribution of the VEP over the scalp. But such inferences have not been made in this thesis. All investigations of scalp distribution are concerned with the relative distributions due to different stimuli, not with the absolute locations on the scalp. And no conclusions drawn in this thesis depend on the reference electrode being perfectly neutral.

CHAPTER 3

(Results 1)

To what extent do motion-reversal VEPs reflect the activity of direction-selective mechanisms?

The stimulus chosen for most detailed investigation was the reversal of direction of motion of a visual noise pattern. Motion-reversal has the advantage that it is less likely than other movement time-functions to evoke response components from mechanisms insensitive to the direction of motion (see chapter 1). Noise was used rather than a periodic pattern to avoid the various effects that can occur when viewing periodic patterns: complementary after images (MacKay, 1957a, b), adaptation to a particular spatial frequency (Blakemore & Campbell, 1969b; Campbell & Maffei, 1970) and reversed motion and standstill effects (Schouten, 1967; Foster, 1968). One standard grain-size of noise was used in most experiments (Fig. 2.2.1). This size was chosen on the basis of some preliminary experiments so as to give large VEPs for a stimulus velocity of 10^{o}/sec.

One might expect that the motion-reversal VEP would arise purely from direction-selective neural processes, since the only parameter that changes at reversal is the direction of movement. In fact, however, there are a number of possible ways in which direction-insensitive processes might contribute to the VEP. The work of Rietveld & MacKay (1969a, b) suggests that the motion-reversal VEPs are not merely the response of pattern-appearance detectors (section 1.1), but certainly does not rule out the possibility that there is some contribution from

direction-insensitive processes. The question is investigated in detail in this chapter.

Before the possibility of such artifacts is discussed, however, some evidence is presented that direction-selective processes do make at least some contribution to the motion-reversal VEP.

3.0.1. Direction adaptation.

Psychophysical evidence suggests that there may exist movement-sensitive mechanisms which are subject to adaptation following prolonged stimulation by movement in the direction to which they are most sensitive (e.g. Wohlgemuth, 1911; MacKay, 1961a; Sekular & Ganz, 1963; Sekular & Pantle, 1966; Pantle & Sekular, 1969). There is also physiological evidence for this, at least in rabbit (Barlow & Hill, 1963b). Experiments were therefore carried out to investigate whether any indications of such adaptation are detectable in the motion-reversal VEPs.

The subject saw the noise pattern move steadily in one direction for, typically, 10 secs., then it changed to a periodic reversing motion for, typically, 5 secs., then steady motion again and so on.

It was found that the motion-reversal VEPs were indeed affected by the direction of the steady (adapting) motion. This effect was never very great, and it was sometimes so slight as to be scarcely significant, especially when the repetition period of the reversing movement was long; but for shorter repetition periods the effect was clearly detectable (Fig. 3.0.1).

For subject D.W., when the adapting motion was towards the left, the negative peaks at 0, 200 and 400 msecs were larger than those at

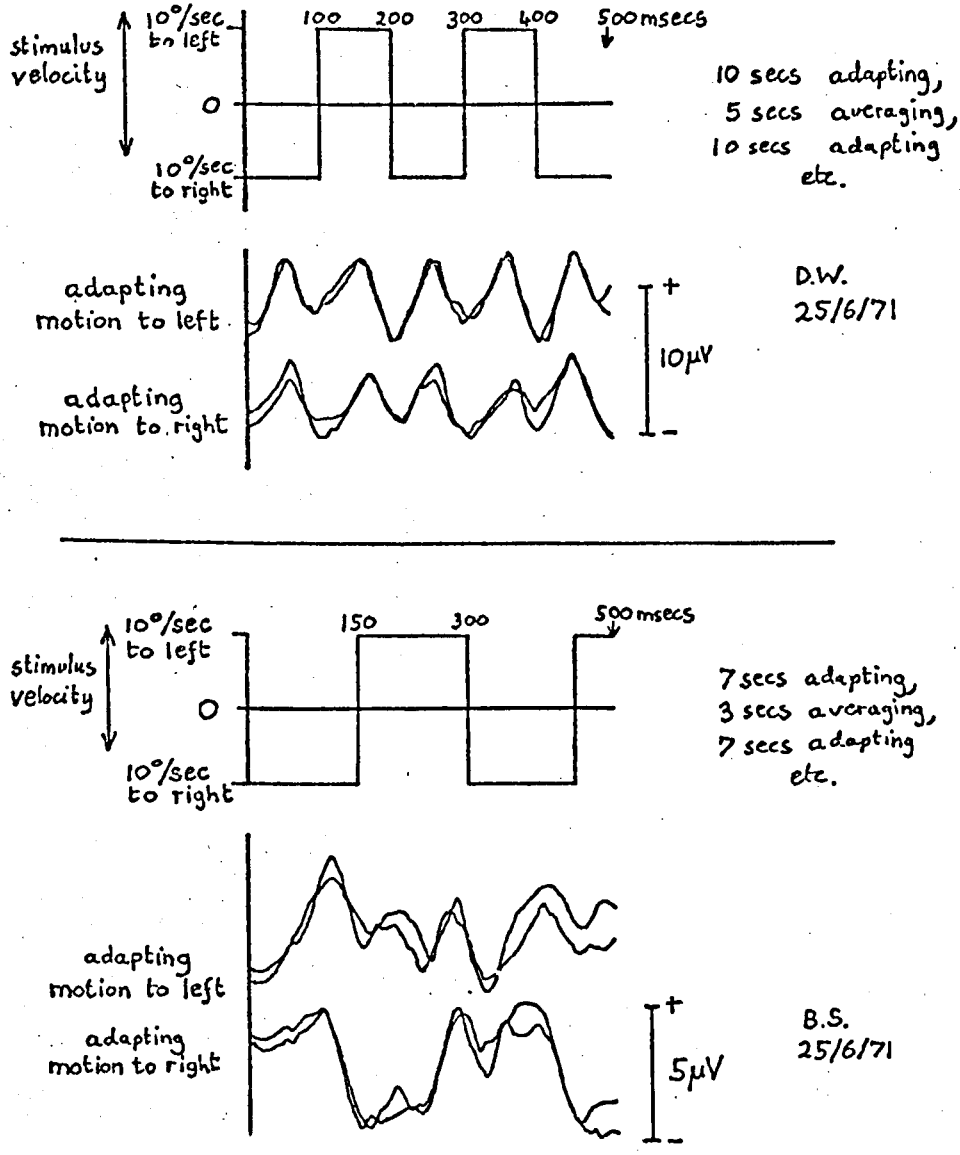


Fig.3.0.1. Directional adaptation.

Periodically reversing stimuli were used, with reversal every 100msecs (D.W.) or 150msecs (B.S.). (The reason for this is explained in the text). With these fast repetition rates, successive responses ran into each other so that individual components could not be clearly identified. But there is no doubt that the responses were affected by the direction of the adapting motion.

100, 300 and 500 msecs, but when the adapting motion was towards the right the 100, 300, 500 msec. peaks were larger.

For subject B.S., the effect is less easily described, but it can clearly be seen from the figure (3.0.1) that the motion-reversal VEPs were substantially different for the two directions of the adapting motion.

Since every stimulus parameter except the direction of the adapting velocity was kept constant in this experiment, it may be assumed that the difference between the VEPs for the two directions of adapting velocity was caused by the adaptation of mechanisms in the brain sensitive to the direction of stimulus motion.

It follows that direction-selective mechanisms contributed to the motion-reversal VEPs; and specifically by virtue of their direction-selectivity. The following sections report experiments to investigate possible additional contributions.

3.1. Are there artifacts due to slowing down at reversal?

Motion-reversal takes a finite time (5 msecs approx.), and this could cause a change in the activity of neural mechanisms irrespective of whether they were direction-selective. In particular, it is known that psychophysically measured contrast sensitivity is higher for slowly ($\sim$1 °/s) moving objects or stationary ones than for faster moving objects (Van Nes, 1969). The temporary slowing down at the moment of reversal might therefore produce a brief increase in effective contrast, evoking a response from neural mechanisms sensitive to pattern contrast but not necessarily sensitive to motion direction.

The work of Rietveld & MacKay (1969a, b) which was discussed in chapter 1, suggests that the motion-reversal VEP may not be purely the product of the mechanisms which cause the pattern-appearance VEP, but it certainly does not rule out the possibility that some components of the two kinds of VEP share the same origin. The experiments described in this section were designed to investigate whether processes insensitive to direction contribute to the motion-reversal VEPs as a result of the brief slowing down at reversal.

3.1.1. Tachistoscopic motion-reversal.

First, the tachistoscope was used to produce motion-reversal without the moving pattern slowing down. The results for six subjects are shown in Figs. 3.1.1 - 3.1.3. There was a difference between the VEP for tachistoscopic motion-reversal and the control, (both patterns moving in the same direction) but it was not great; and in both cases the main VEP components were much smaller than in the VEP evoked by mirror-produced motion-reversal. The first VEP component was reduced in amplitude less than the later ones. It might be inferred that a major part of the latter VEP results from the slowing down at reversal; but it is also possible that the change of noise pattern at the moment of tachistoscopic reversal suppresses the VEP in some way, perhaps related to the elevation of visual threshold by displacement of retinal image reported by MacKay (1970). More experiments were therefore carried out to decide between these alternatives.

3.1.2. Mirror-driven reversal; variation of the turn-round time.

Under normal circumstances mirror-produced motion-reversal

Figs 3.1.1 -3.1.3

A: tachistoscopic motion-reversal.
B: control (no reversal).
A-B: the difference between the VEPs to reversal and the control.
C: mirror-produced reversal.

The arrows indicate the direction of motion before and after reversal. Two responses, each the mean of 100 samples, are superimposed to indicate variability.

Velocity = 10°/sec.

Lower half-field(4° radius) was used, as always unless otherwise stated.

Note that for subjects (B.S.,C.D.,H.H.) who gave a prominent 100msec positive peak in the mirror-produced reversal VEP, there was also a corresponding, though smaller, 100msec positive peak in the tachistoscopic reversal and control VEPs. But later peaks in the mirror-produced VEPs did not have such obvious counterparts in the tachistoscopic VEPs.

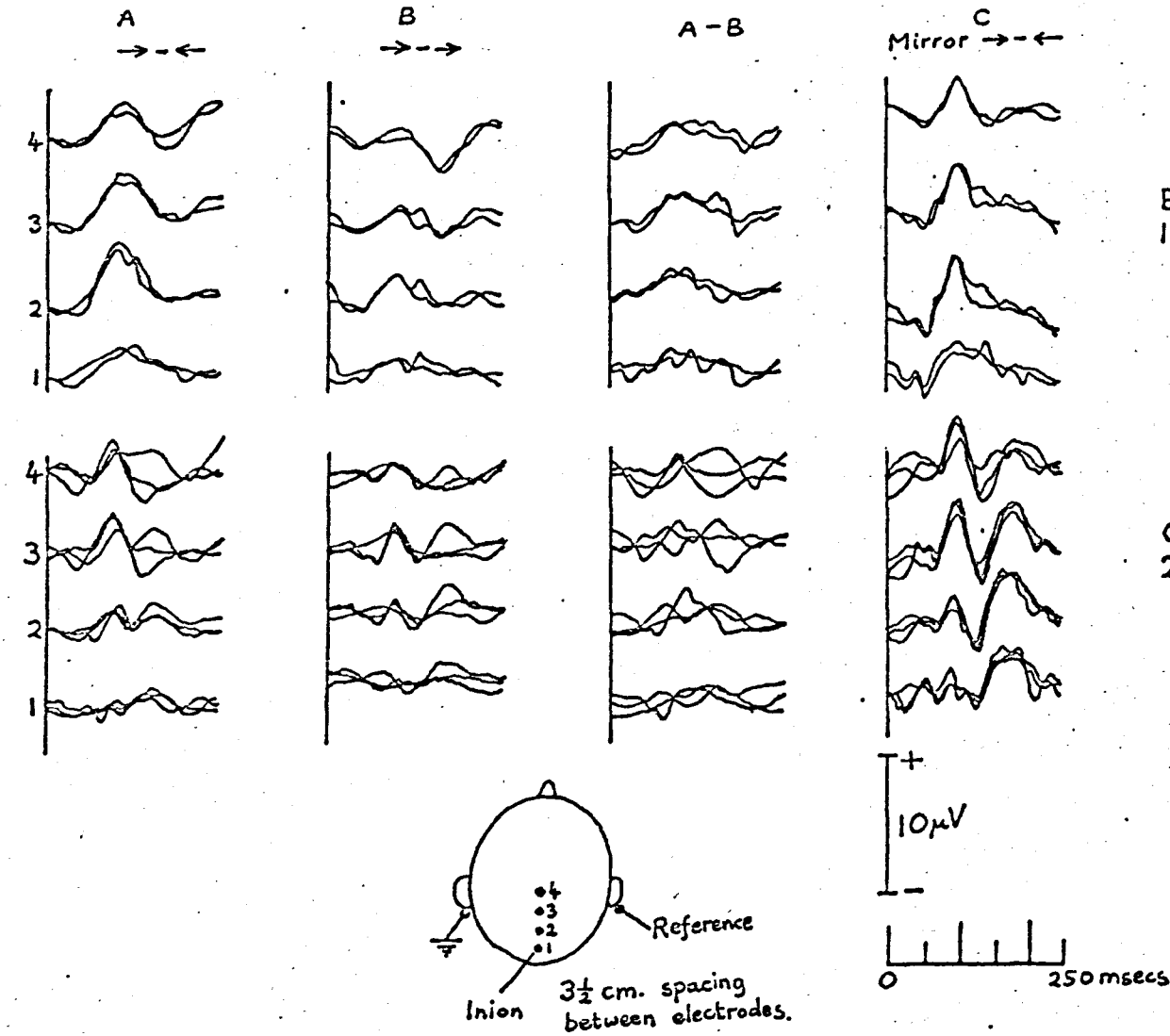

A
B
A-B
C
Mirror
4
3
2
1
B.S.
14/11/70
C.D.
21/11/70
+
10μV
−
0
250 msecs
Reference
Inion
3½ cm. spacing
between electrodes.

Fig. 3.1.1

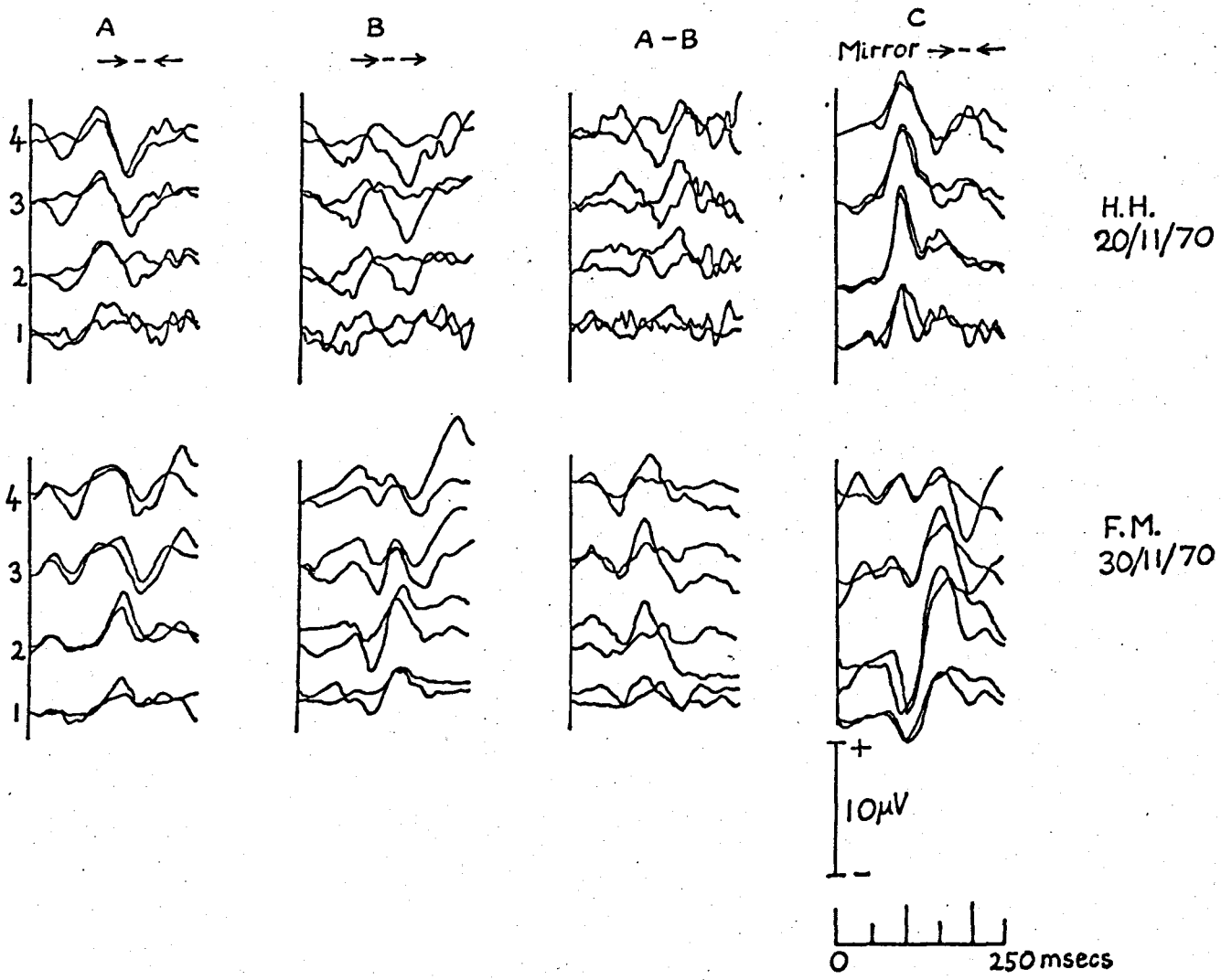


Fig. 3.1.2

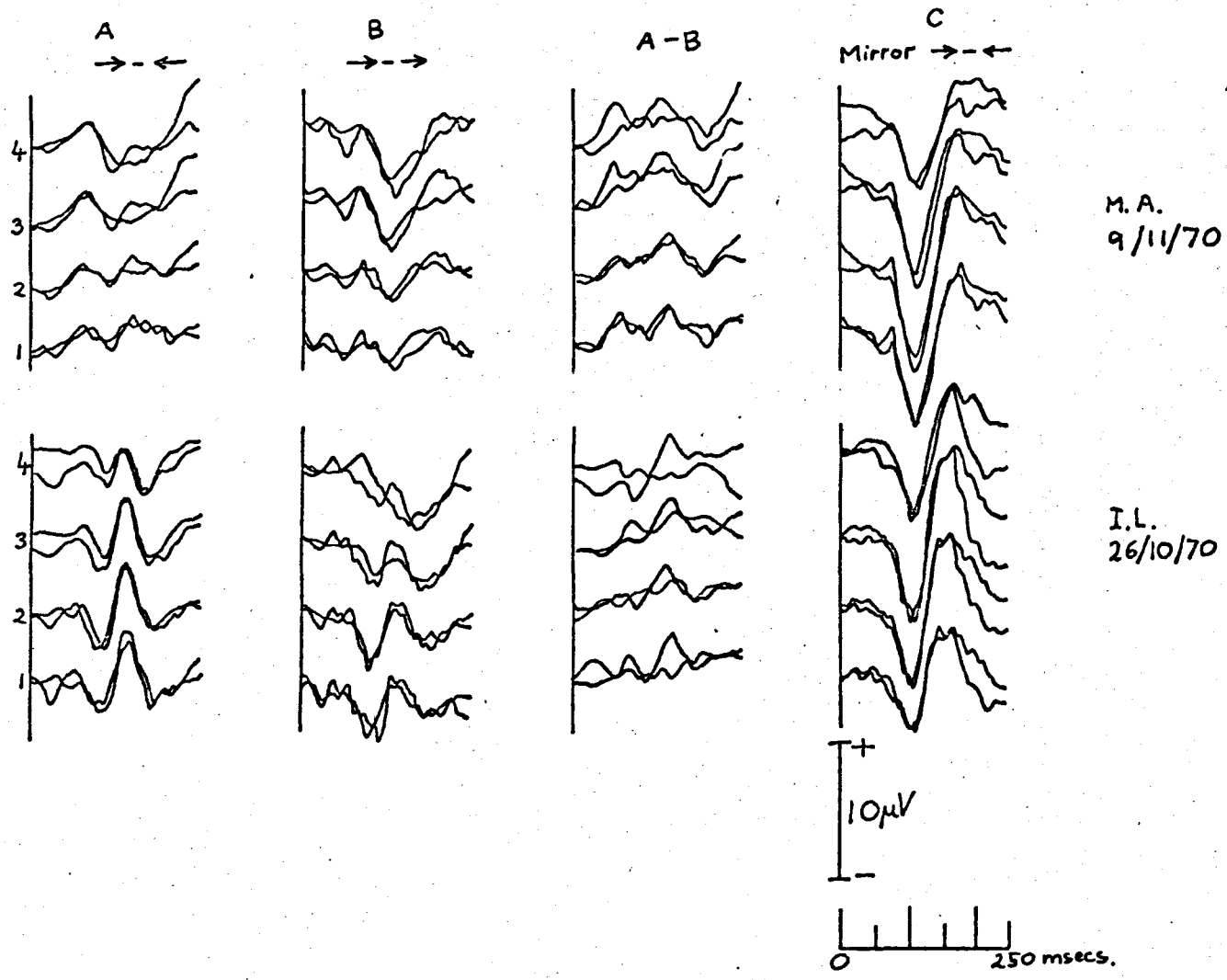


Fig. 3.1.3

was completed within 5 msecs. If any components of the motion-reversal VEP were caused by increased effective contrast due to slowing down at reversal, then lengthening the turn-round time above 5 msecs. should increase these components and thereby modify the VEP. (It is unlikely that the effect of increasing the turn-round time would have reached saturation by 5 msecs., for I have found that VEPs to pattern-appearance do not reach saturation until the exposure duration reaches 10 - 40 msecs., for the same pattern-contrast and luminance as in the motion-reversal experiments. Checkerboard-reversal VEPs are reported to be largest if the alternation pulse lasts 30 msecs (Cobb et al., 1968).) The signal controlling the mirror movement was therefore passed through a simple RC low-pass filter with variable time contrast, to increase the turn-round time. Time constants between 2.8 and 18 msecs were used, corresponding to turn-round times between 8 and 50 msecs, but it can be seen from Figs. 3.1.4 - 3.1.6 that the VEP was not greatly affected by these increases in the turn-round time. Subject C.D. does, it is true, show an increase in the negative 140 msec peak for time constants of over about 10 msecs, but these correspond to an increase in turn-round time by a factor of six or more, and there is no detectable effect for smaller increases. This experiment was carried out fully on five subjects, and partly on two more, with no contradictory results. Subjectively, the increased turn-round time was not noticeable, and there was never any discernible increase in apparent contrast at the moment of reversal.

To reduce the turn-round time below 5 msecs, wave-shaping was applied to the mirror-control waveform, as outlined in section 2.2.1.

Figs 3.1.4 - 3.1.6. Variation of the turn-round time.

Velocity = 10°/sec.

The VEPs were not greatly affected by the increases in the turn-round time.

For subject C.W. there is considerable noise at the more anterior electrodes (3,4) due to alpha activity. This does not make the results hard to interpret, however, because the VEP is largest at the posterior electrodes (1,2). In most subjects the alpha rhythm did in fact predominate at electrodes anterior to those at which the motion-reversal, -onset and -offset and pattern-appearance VEPs were largest.

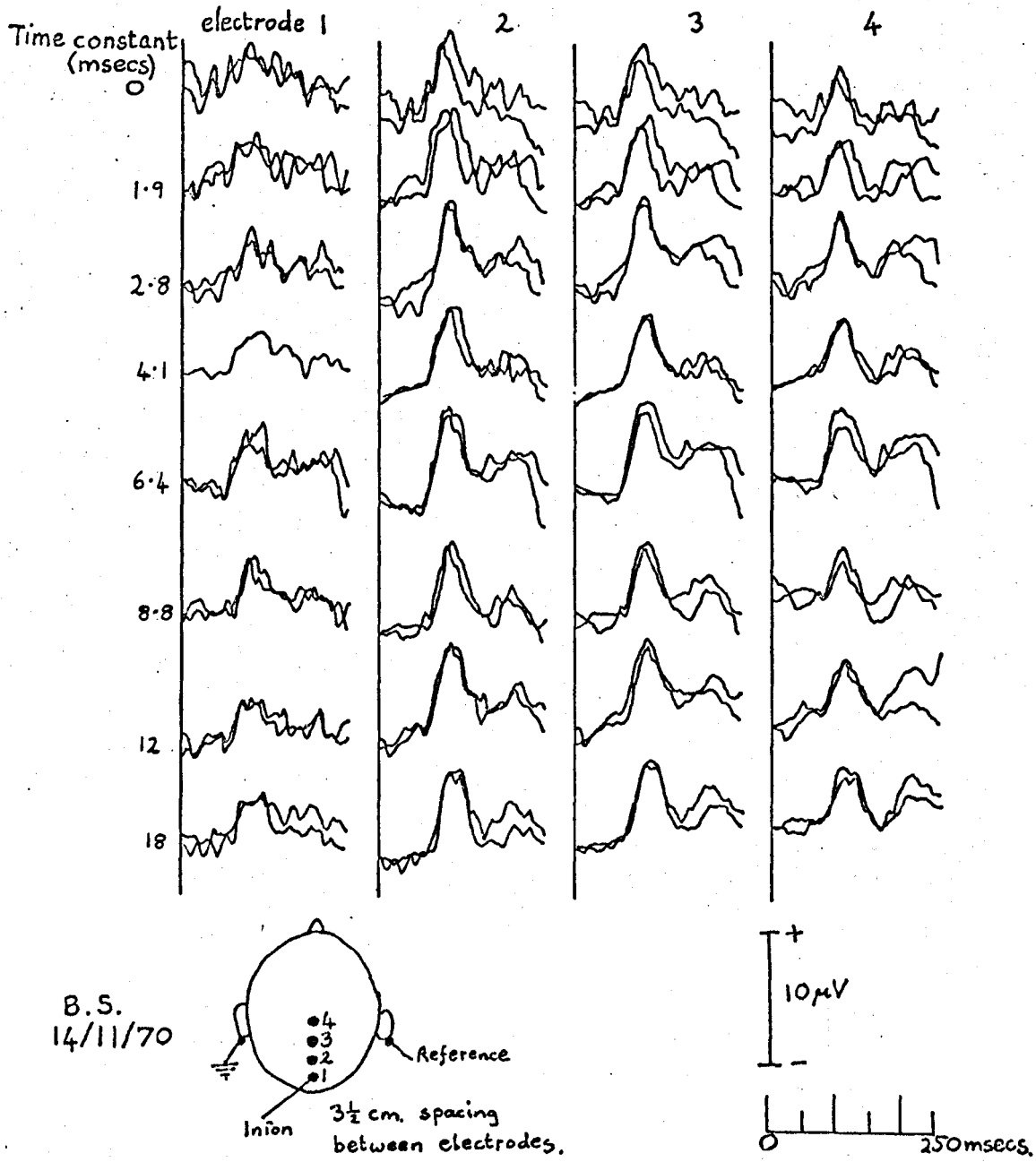

Time constant (msecs)
electrode 1
2
3
4
0
1·9
2·8
4·1
6·4
8·8
12
18
B.S.
14/11/70
4
3
2
1
Reference
Inion
3½ cm. spacing between electrodes.
+
10μV
−
0
250msecs.

Fig. 3.1.4

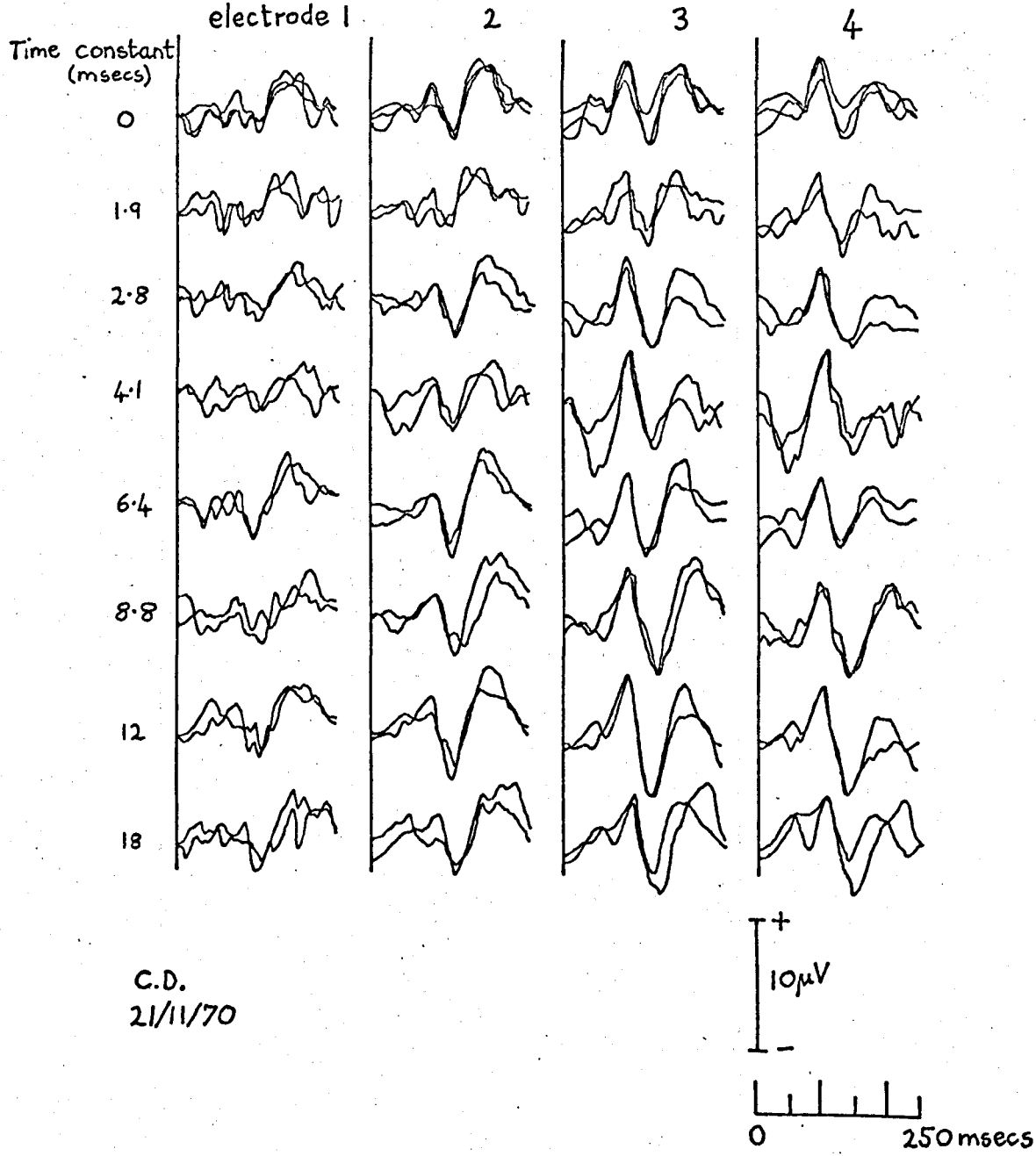

electrode 1
2
3
4
Time constant (msecs)
0
1·9
2·8
4·1
6·4
8·8
12
18
C.D.
21/11/70
+
10μV
−
0
250 msecs

Fig. 3.1.5

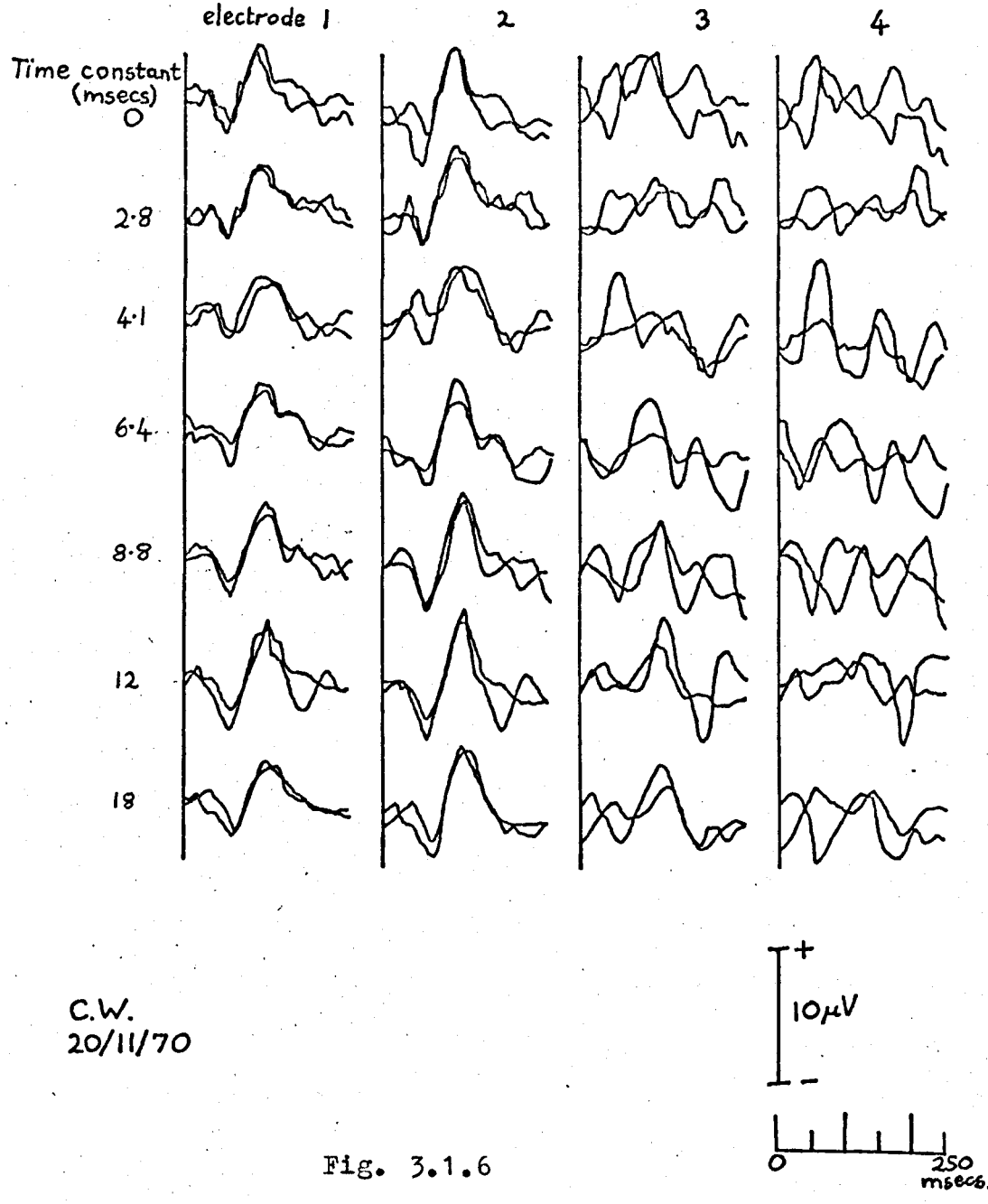

electrode 1
2
3
4
Time constant (msecs)
0
2·8
4·1
6·4
8·8
12
18
C.W.
20/11/70
+
10μV
−
0
250
msecs.

Fig. 3.1.6

A shaping pulse slightly larger than the theoretical minimum required for instantaneous reversal (section 2.2.1) had no measurable effect on the VEP (Fig. 3.1.7).

These results suggest that the slowing down at reversal was not responsible for any major components of the (mirror-driven) motion-reversal VEP. This implies that the reduction in the VEP with tachistoscopic motion-reversal was caused by the change of pattern at the moment of reversal rather than by elimination of the slowing down.

3.1.3. Variation of the velocity.

Although the VEP was insensitive to the time-course of motion-reversal, Figs. 3.1.8a, 3.1.9a show that it was very sensitive to the steady velocity before and after reversal, being virtually abolished when the velocity was very high (90°/sec). This reduction in VEP with increased velocity was not due to the decrease in the time of slow movement at reversal, for the addition of a low pass filter of 18 msec time constant (as previously) had no great effect on the 90°/sec VEP (Figs. 3.1.8b, 3.1.9b). Yet the time-course of reversal (within a few msecs of reversal) at 90°/sec with the filter added was very similar to that at 8°/sec with no filter (see Appendix 1).

These findings support the conclusion of the previous section that slowing down at reversal does not cause any major VEP components. The range of velocities for which the VEP is relatively large is within the bounds of what might be expected on the basis of the sensitivity to different stimulus velocities of single units in cat and monkey. For

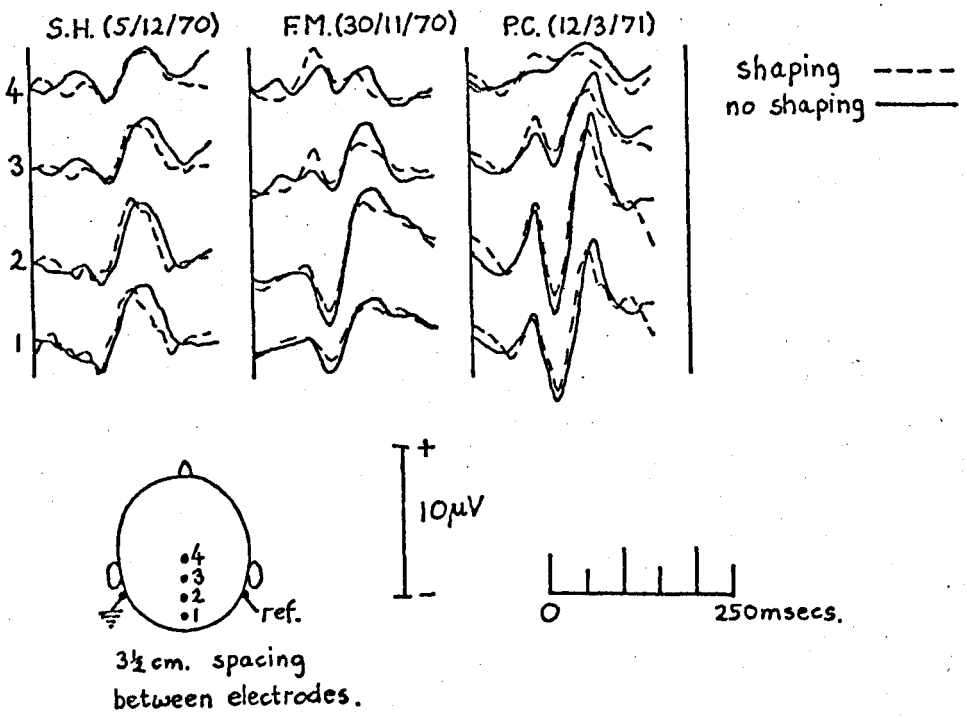


Fig. 3.1.7. The effects of reducing the turn-round time by means of pulse-shaping. There is no significant change in the VEPs. Velocity = 10°/sec. Each trace is the mean of 200 samples. The standard deviation between averaged responses is about 0.5μV for each subject.

Figs 3.1.8 - 3.1.9

a) The effect of varying the velocity.

b) The effect of adding a simple low-pass filter of 18msec time-constant when velocity = 90°/sec.

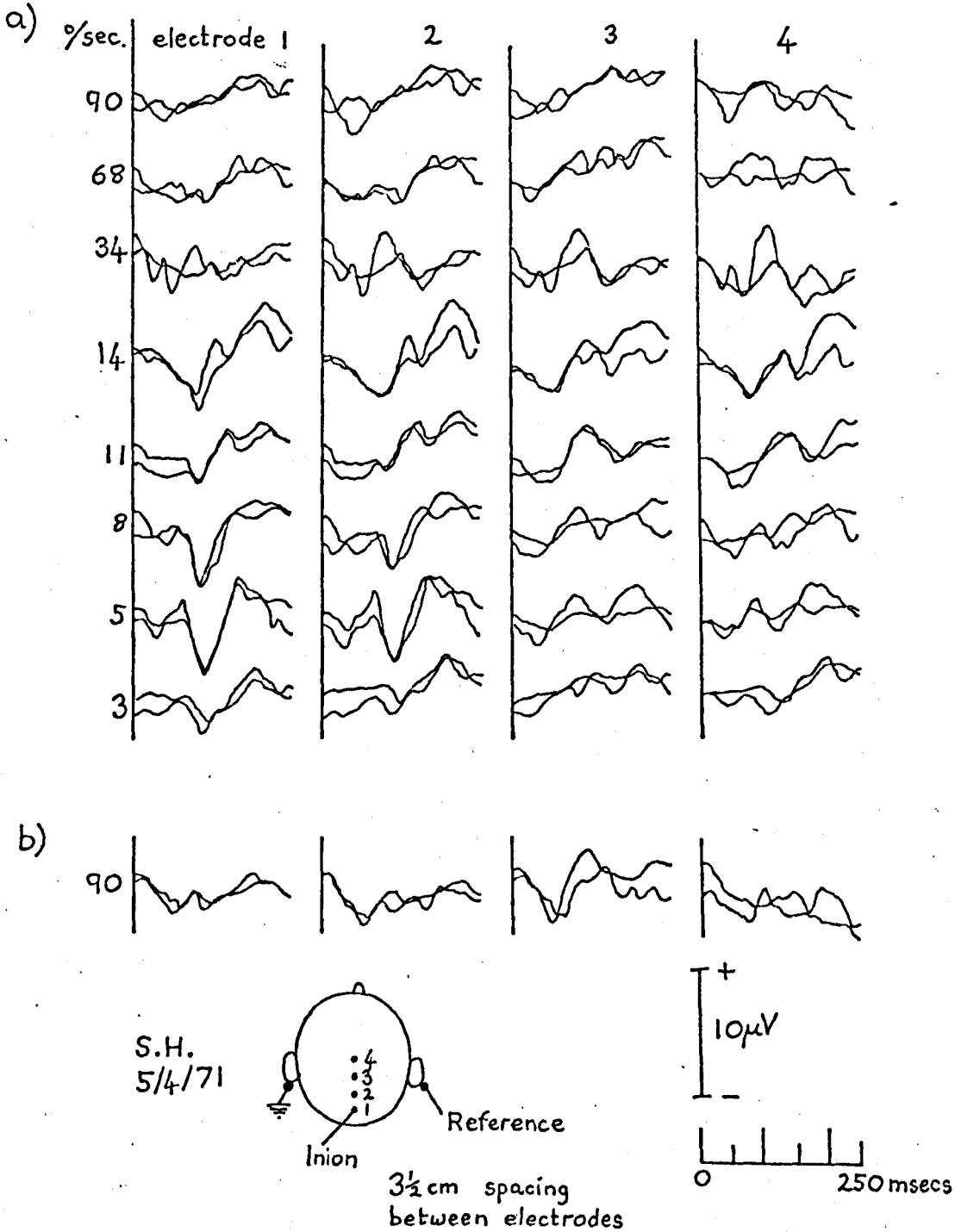

a)
%/sec.
electrode 1
2
3
4
90
68
34
14
11
8
5
3
b)
90
S.H.
5/4/71
4
3
2
1
Inion
Reference
3½ cm spacing
between electrodes
+
10μV
−
0
250 msecs

Fig.3.1.8

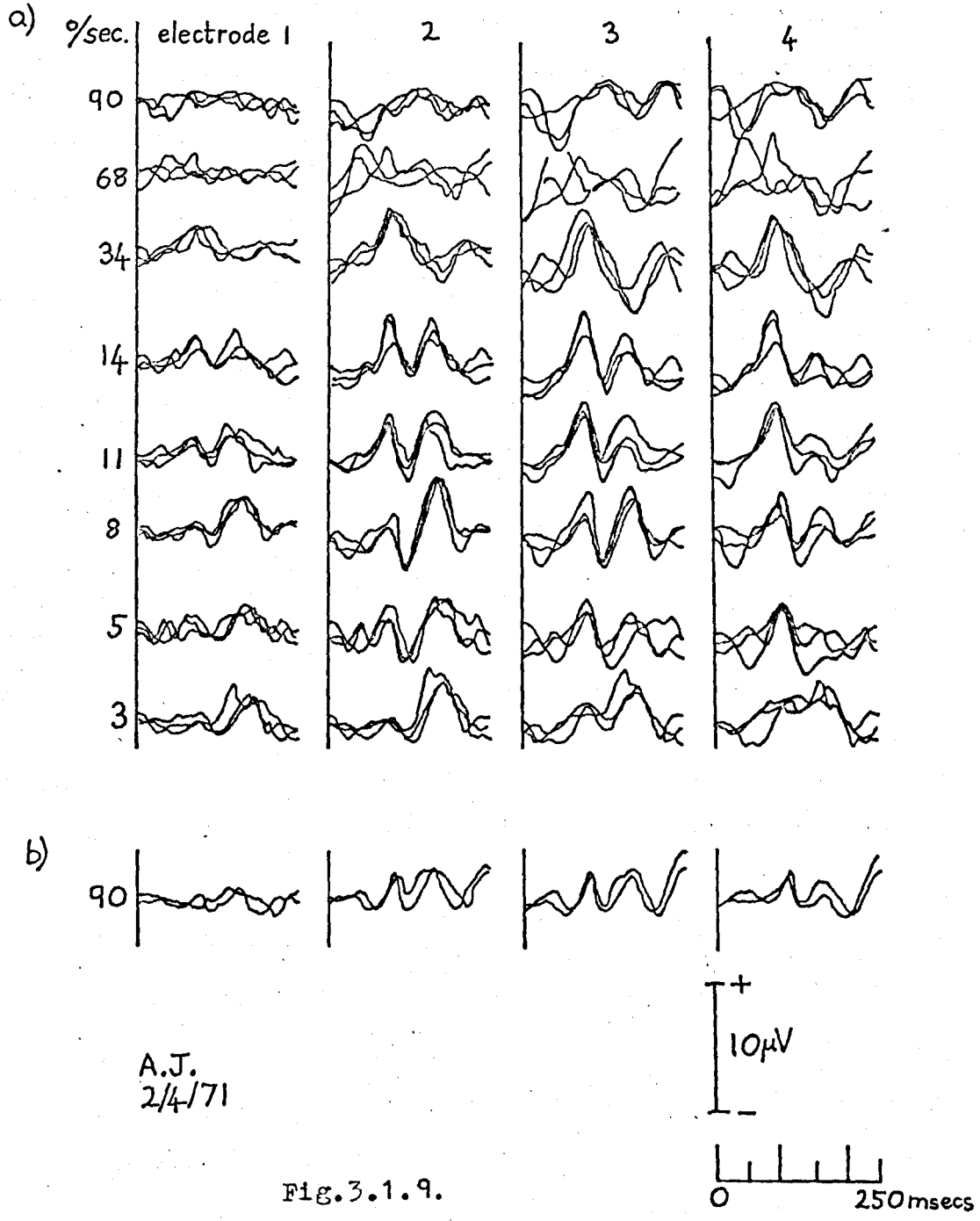

a)
%/sec.
electrode 1
2
3
4
90
68
34
14
11
8
5
3
b)
90
+
10μV
−
A.J.
2/4/71
0
250msecs

Fig.3.1.9.

Pettigrew, Nikara & Bishop (1968) found that the optimal velocity of stimulus motion was 4°/sec, on average, for single neurones in cat striate cortex; but their criterion for optimal velocity was the total spike discharge count, a criterion which is biased in favour of low velocities (see section 1.3). And Wurtz (1968a, b) found that most units in monkey striate cortex responded best for velocities below about 100°/sec. In extra-striate of cat, complex cells respond best for velocities between 0.1 and 20°/sec (Hubel & Wiesel, 1965). (See section 3.1 of this thesis for a further discussion of optimal stimulus velocities).

The results in this sub-section were repeated for five subjects, although the 18 msec filter was not used for one of these. The effects of varying velocity are dealt with further in chapter 4.

3.1.4. Comparison of pattern-appearance VEPs for both stationary and moving patterns.

Using the tachistoscope, VEPs to the appearance at constant luminance of stationary and moving patterns were recorded. The results confirmed those of Jeffreys (1970b, 1971) that for stationary patterns the VEP is normally triphasic with positive peaks at about 80 and 180 msecs and a negative peak at about 110 msecs (for the lower half-field). With moving patterns, it was found that for long ($\sim$ 200 msec) exposure durations, the later peaks, especially, were often greatly reduced. But for exposure durations of 10 msecs or less the VEPs to stationary and moving (8 - 10°/sec) patterns were almost identical (Fig. 3.1.10). That is not surprising, since for exposure durations less than about 30 msecs

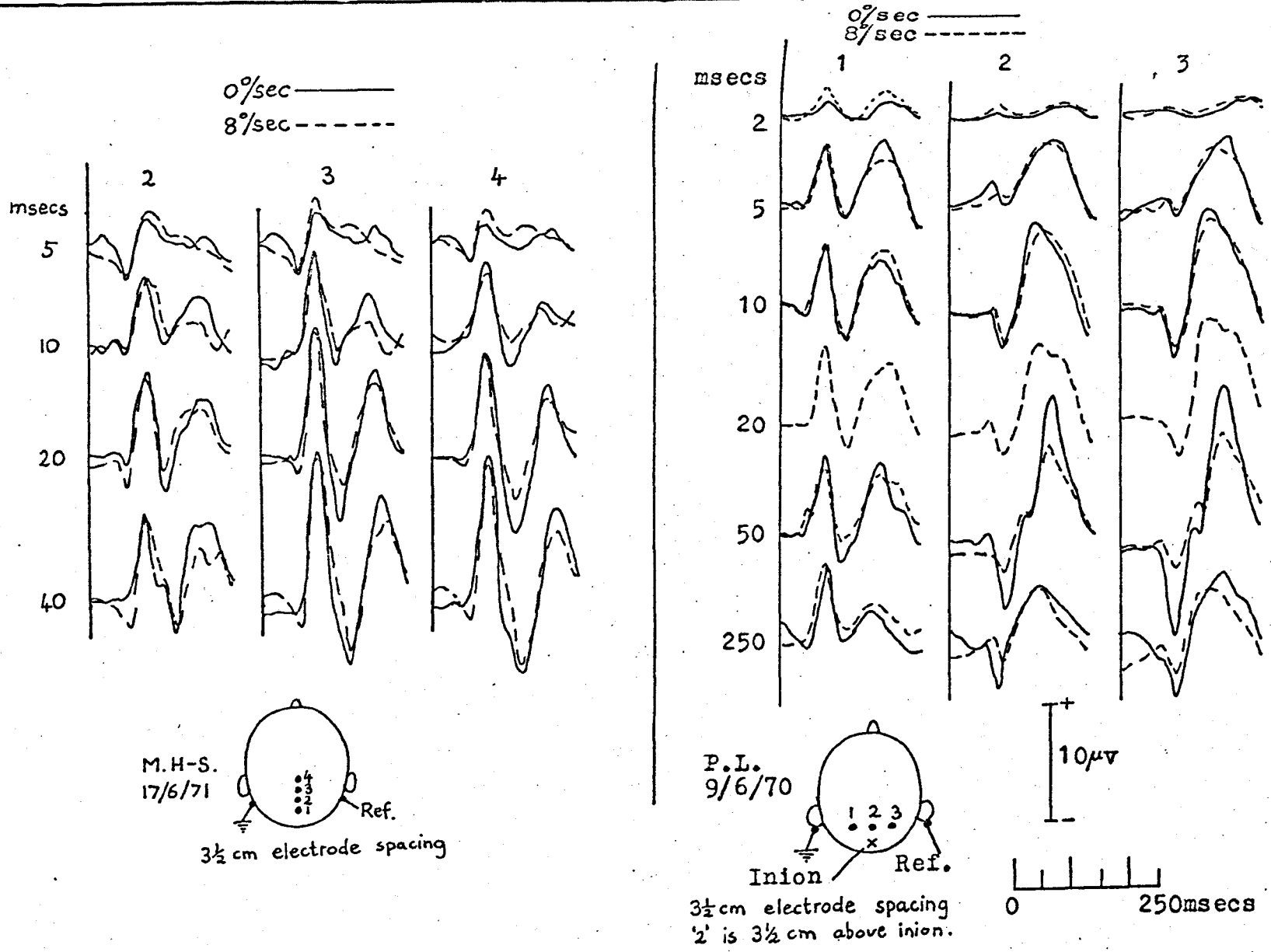


Fig.3.1.10. Comparison of the VEPs to the appearance of stationary and of moving patterns for various exposure durations.

it was not possible to see clearly whether the pattern was moving. But since the VEPs to brief (10 msec) pattern-appearance were not significantly affected by the motion of the pattern, it would seem unlikely that the change in effective contrast due to an even briefer (less than 5 msec) slowing down at reversal would have evoked a significant VEP. This supports the conclusions of the previous sub-sections.

The above experiments were carried out on four subjects, with the same basic result in each case.

3.1.5. Suppression due to a step-displacement added to the motion-reversal.

The inference suggested by the last three sections is that the reduction of the main components of the VEPs to tachistoscopic motion-reversal, as compared with those to mirror-driven reversal, was caused by the change of pattern rather than by the momentary slowing down at reversal. A change of noise pattern is statistically equivalent to a large displacement of the pattern, so the effect of a step-displacement in addition to motion-reversal was studied.

This did indeed suppress the VEP if the step occurred within about 20 msecs of the moment of reversal (Figs. 3.1.11 - 3.1.12), which confirms the above interpretation, as suppression took place even when the time-course of reversal was not affected. The suppression was usually greater for a step occurring 10 or 20 msecs after the moment of reversal than for one an equal time before reversal (Figs. 3.1.11 - 3.1.12).

Step-displacements as small as 9' or 10' often produced significant suppression of the VEP, but the degree of suppression increased with the size of step (Figs. 3.1.13 - 3.1.14).

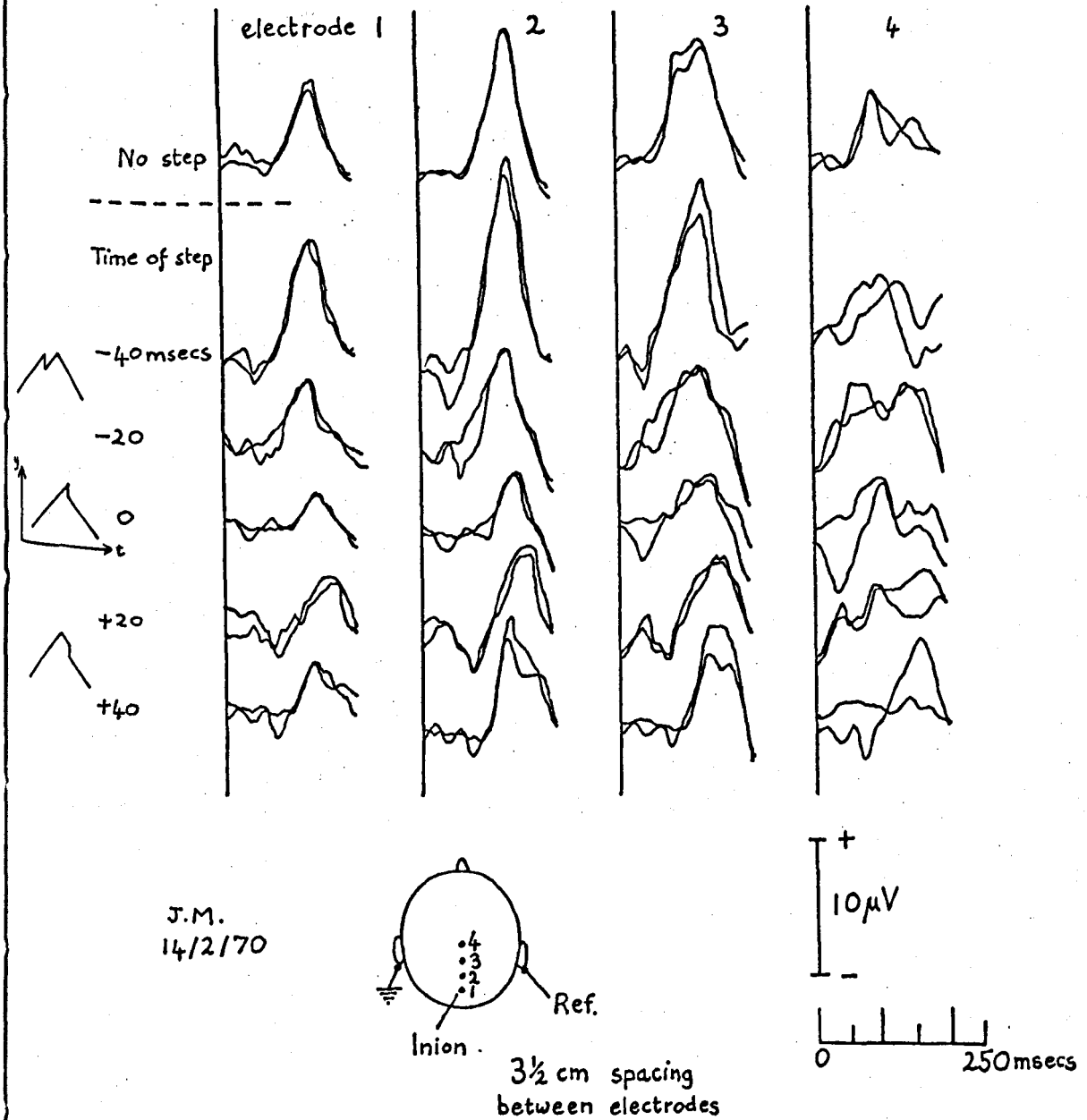


Fig.3.1.11. The effects on the VEP of a step-displacement superimposed on the motion-reversal waveform, for various moments of occurrence of the step. Step size = 1°. Velocity = 10°/sec.

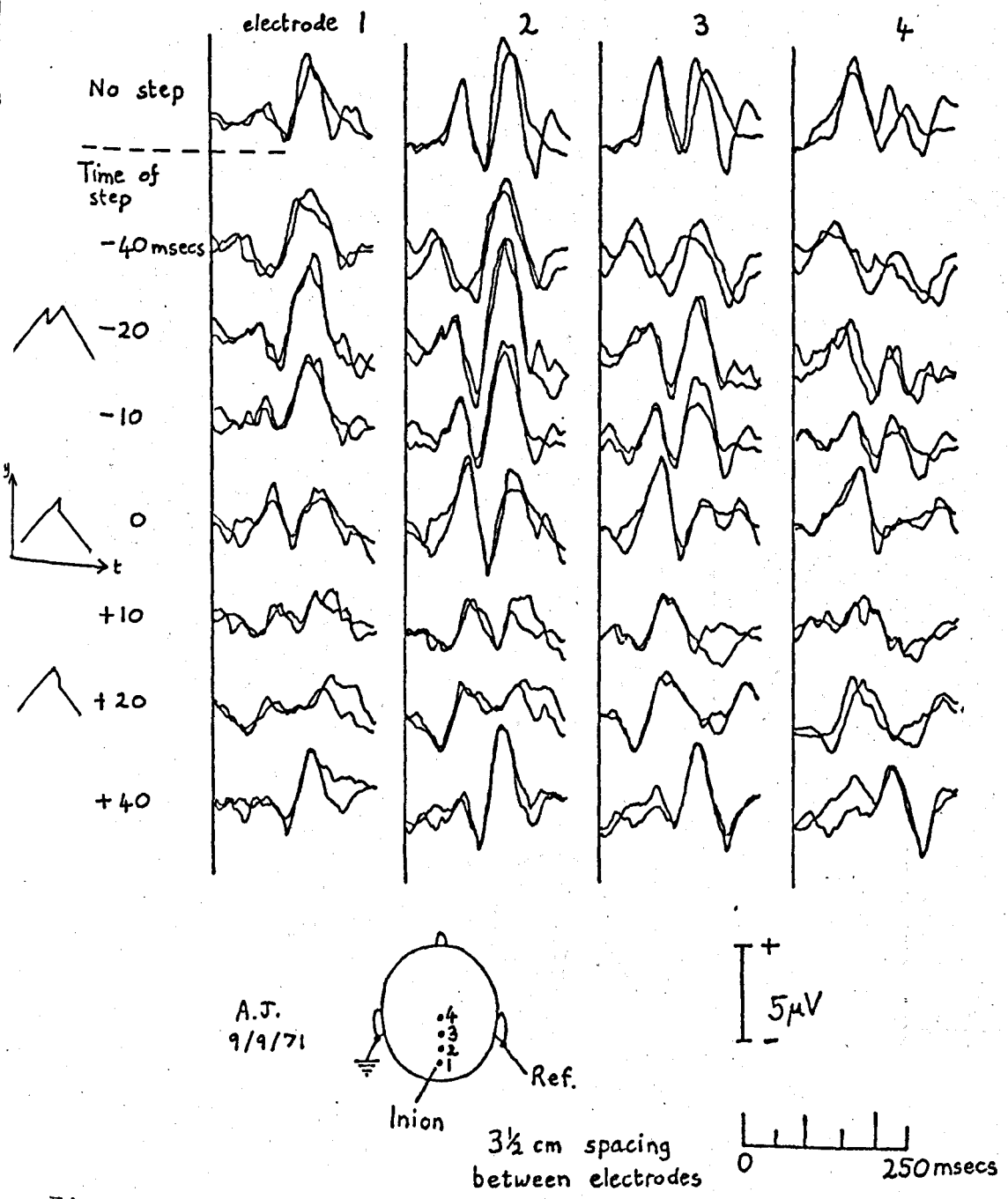


Fig.3.1.12. The effects on the VEP of a step-displacement superimposed on the motion-reversal waveform, for various moments of occurrence of the step. Step size = ½°. Velocity = 8°/sec.

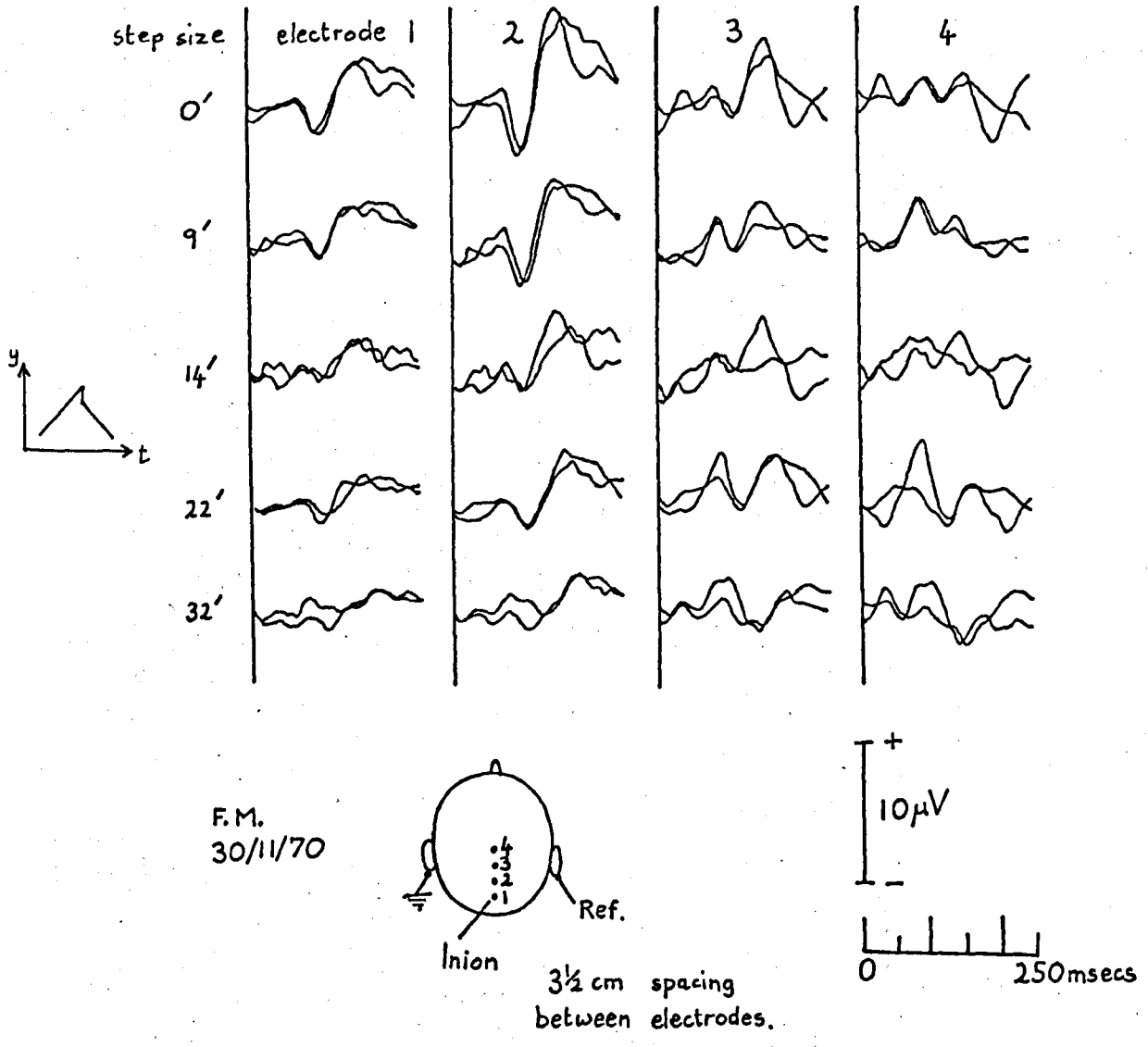


Fig.3.1.13. The effects on the VEP of a step-displacement superimposed on the motion-reversal waveform at the moment of reversal, for various step sizes.
Velocity = 10°/sec.

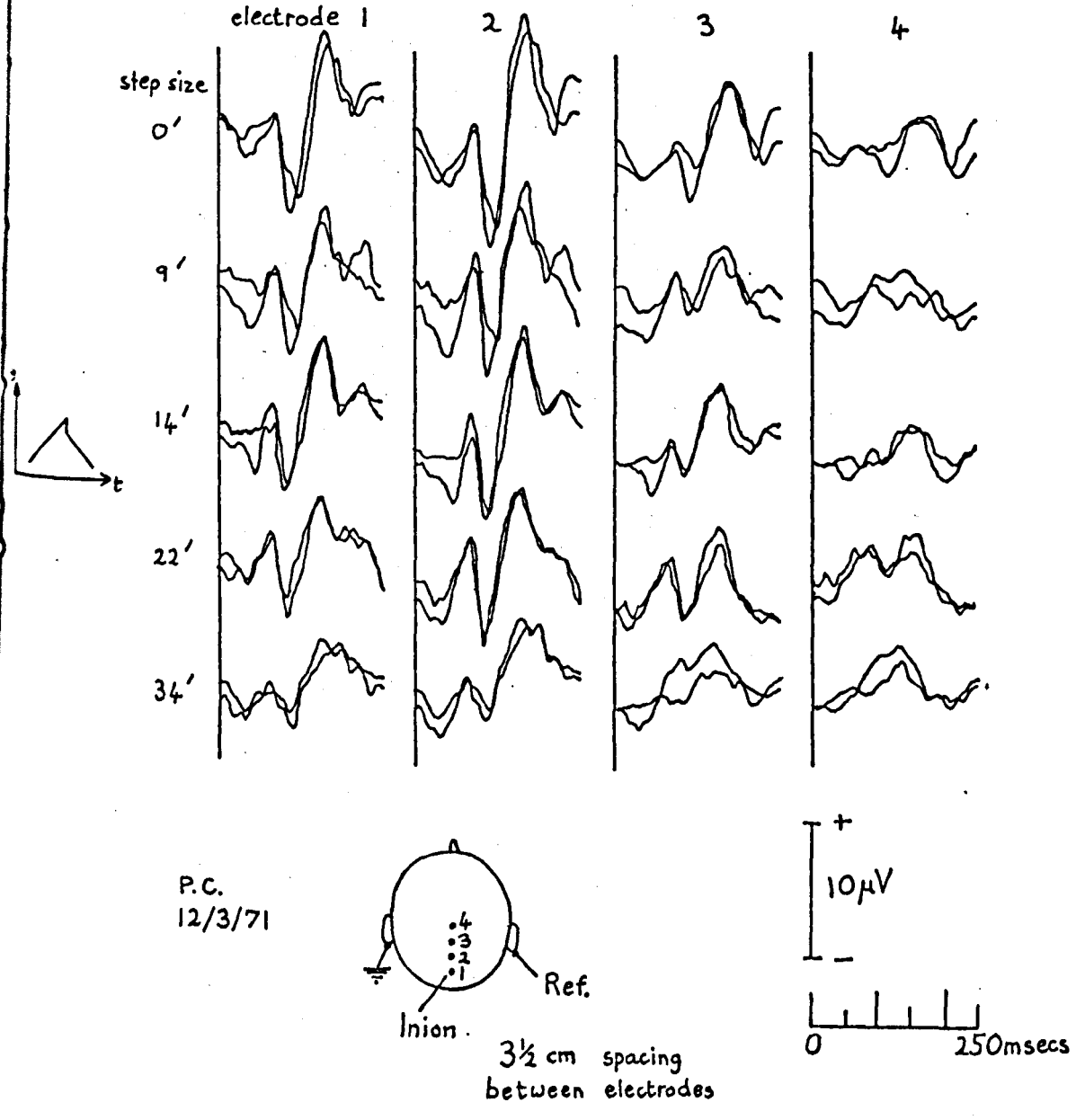


Fig.3.1.14. The effects on the VEP of a step-displacement superimposed on the motion-reversal waveform at the moment of reversal, for various step sizes. Velocity = 10°/sec.

Reversing the direction of the step-displacement did not greatly change its effect on the VEP if it occurred at the moment of reversal (Fig. 3.1.15). For steps occurring slightly before or after reversal, however, the direction of the step-displacement tended to be rather more important, but this has not been investigated in detail.

As in the case of tachistoscopic motion-reversal (sub-section 3.1.1), the early positive VEP component appeared to be less susceptible to suppression than did the later components. For example, in Fig. 3.1.14 the early positive peak seems to have been slightly enhanced as a result of the step-displacement, although the later peaks were suppressed. The matter was investigated more carefully using two subjects for whom the early positive component was predominant. It was found that a small (15') step-displacement did produce suppression, but a larger one (30' or 1°) did not (Fig. 3.1.16). This appears to be related to the fact that the VEP to a step-displacement during steady motion included a positive VEP component which had the same latency as the early positive component of the motion-reversal VEP, and tended to increase with the size of the step-displacement (Fig. 3.1.16). The failure of large (30' or 1°) step-displacements to suppress the early component of the motion-reversal VEP may, therefore, have been due to an enhancement of this component by a more or less additive interaction with the corresponding component of the VEP to a step-displacement during steady motion. It is emphasized, however, that such a linear or quasi-linear mechanism cannot be the cause of the suppression of the later VEP components. A linear interaction

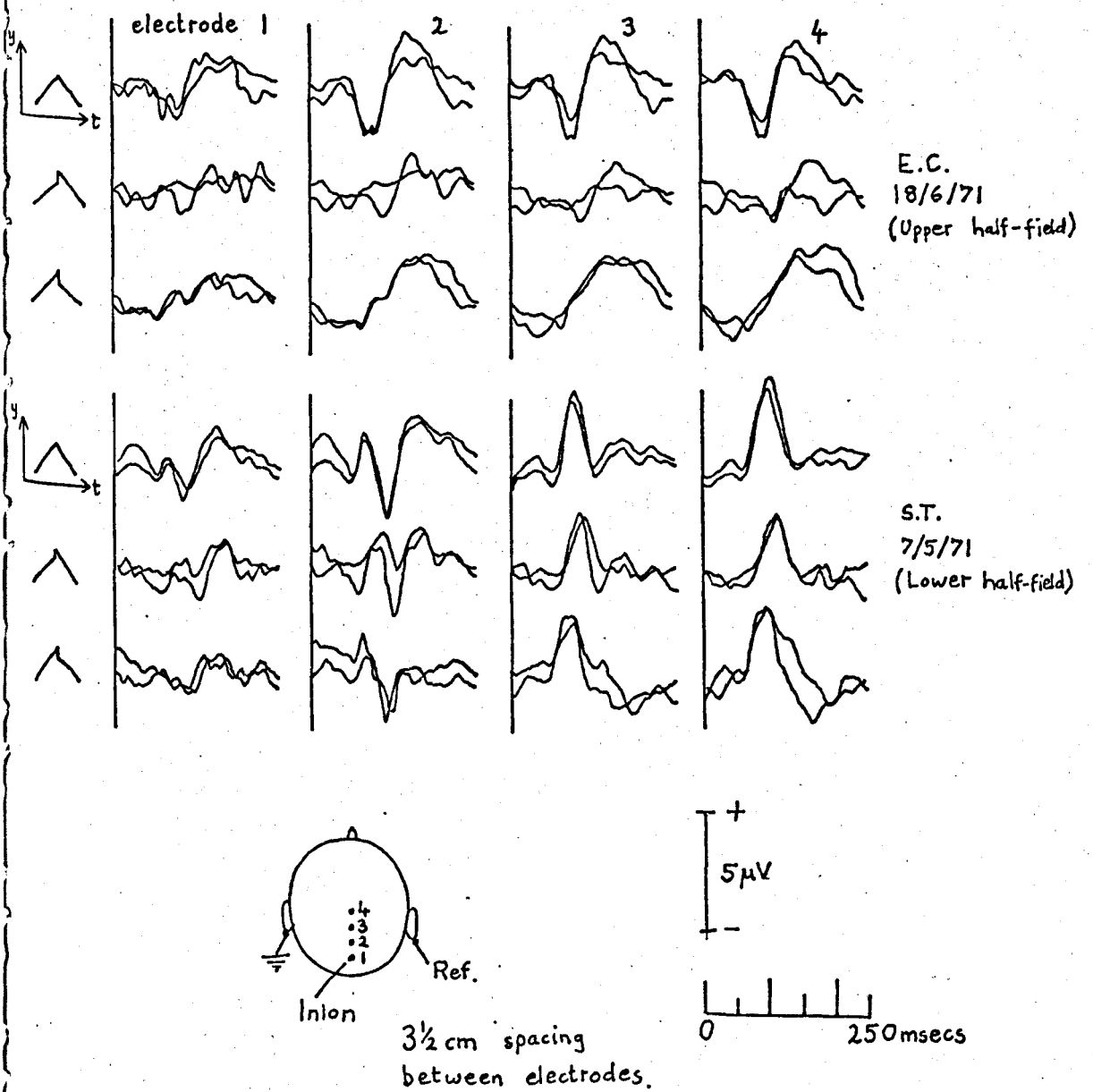


Fig.3.1.15. Comparison of the effects on the VEP of a step-displacement superimposed on the motion-reversal waveform at the moment of reversal, for the two directions of step. Step size = 15'. Velocity = 10°/sec. Similar, though not identical, effects were produced in each case.

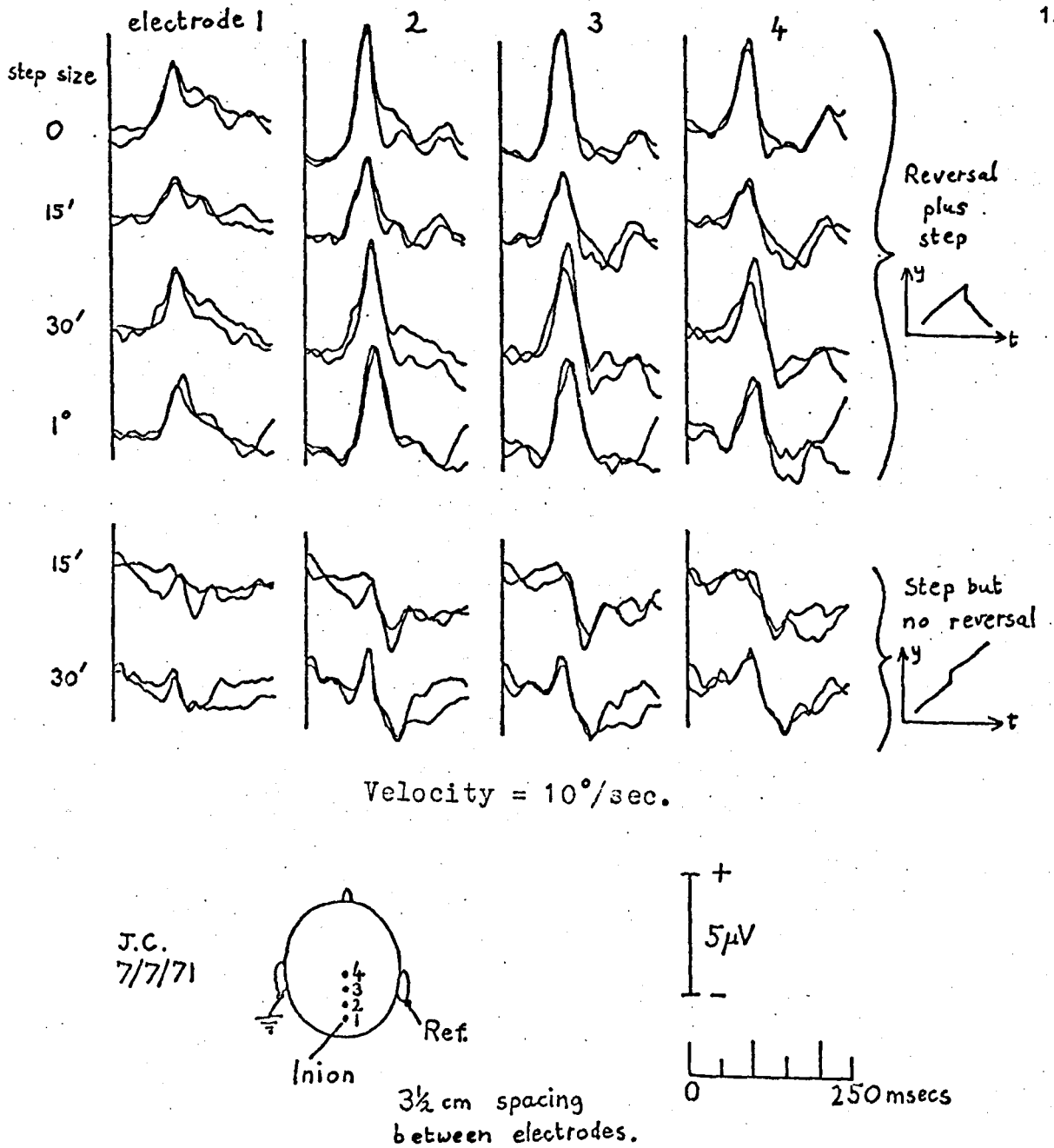


Fig.3.1.16. Apparent lack of suppression of the VEP, with a step-displacement superimposed on the motion-reversal waveform at the moment of reversal. This was only observed for the early positive VEP component, however, and even for this there was suppression if the step-displacement was sufficiently small. These effects may have been caused by a positive VEP component of similar latency which could be evoked by a step without reversal. (See the text).

would have tended to enhance these later components just as it apparently enhanced the first component, for peaks of similar latency in the VEPs to motion-reversal and to step-displacement during steady motion tended to have the same polarity.

The cause of the suppression is not known. It may be related to the discovery of MacKay (1970) that the brightness threshold for detection of a flash is raised by displacement of the surround field. A threshold elevation also occurs due to the sudden displacement of a noise field (MacKay, D.M. personal communication), and due to a tachistoscopic change of noise pattern. MacKay suggested that the effect was probably due largely to the same mechanisms that cause elevation of visual threshold before and during eye movements (e.g. Latour, 1962; Volkmann, 1962), a phenomenon for which there are VEP correlates (Michael & Stark, 1967; Duffy & Lombroso, 1968).

Whether or not the suppression of the motion-reversal VEP is related to the above effects, it is certainly not unexpected that a velocity-detecting system should be adversely affected by a shift or change of pattern, since this will eliminate some of the position-information on which velocity-detection is presumably based. Also, phi movement may be generated (randomly for tachistoscopic reversal) and this may act as noise in the velocity-detection channels.

I have observed a psychophysical phenomenon which may be connected with this. If the mirror system is driven with a tri-angular waveform to produce 10°/sec movement, reversing at regular intervals, motion is observed up to a frequency of about 25Hz, after which only a

slight flickering is detectable. If a large (2^{o}) displacement is added at each moment of reversal, movement-sensation is lost at a much lower frequency, about 12Hz. Similarly with tachistoscopic reversal, 12 Hz is approximately the limit for movement-detection.

3.1.6. The effect of a brief standstill during continuous stimulus motion.

As an additional check that the brief slowing down at motion-reversal was not the cause of any components of the VEP, the effect of a brief standstill during continuous stimulus motion was studied. As shown in Fig. 3.1.17, a standstill of 5 msecs produced only a very slight VEP. This confirms the previous conclusion that the finiteness of the turn-round time was not important.

It should be noted, however, that a standstill of 10 msecs or more did produce a relatively large VEP, and the VEP to standstill for 20 msecs was almost identical to the motion-reversal VEP. The possible significance of this is discussed in chapter 5.

This experiment was performed on only one subject.

3.2. Possible artifacts with an idealised stimulus motion.

The previous section indicates that the finiteness of the turn-round time was not responsible for any major components of the motion-reversal VEP. The stimulus motion can therefore be regarded as a good approximation to the ideal case of instantaneous reversal. But artifacts might occur even with instantaneous reversal, and this possibility is investigated in this section.

3.2.1. Eye movements.

Eye movements might be elicited by motion-reversal, and these

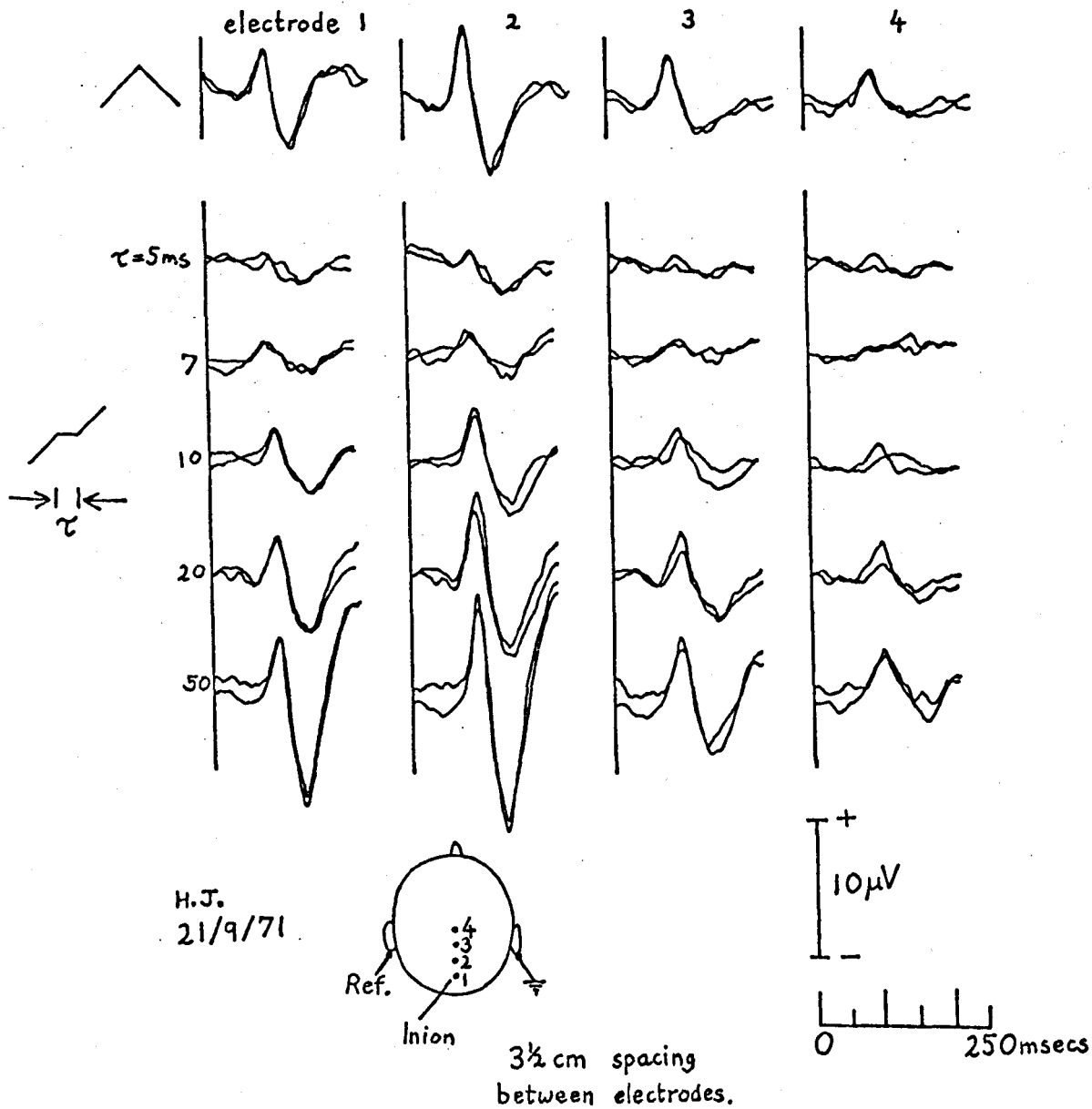


Fig.3.1.17. The VEP to a brief standstill during continuous stimulus motion. Velocity = 10 °/sec. See the text.

might contribute to the VEP in some way. For example, saccadic eye movements over a stationary patterned field produce VEPs (Gaarder et al., 1964; Armington et al., 1967; Gaarder, 1968). It is also claimed that saccadic eye movements suppress the VEP to pattern contrast-reversal (Gross et al., 1967), (but see section 1.1 for criticism of the latter experiment). Now the latency of eye movements to an unexpected stimulus is typically about 200 msecs for saccades and 150 msecs for pursuit movements (e.g. Robinson, 1968), but for a periodic stimulus the average latency can be almost zero (Fender, 1964). It follows that a comparison of pattern motion-reversal VEPs under conditions of periodic and aperiodic stimulation should indicate whether or not eye movements are implicated in the early components of the VEP.

Fig. 3.2.1a shows that there were no significant differences in the first 180 msecs between the VEPs to periodic and aperiodic stimulation for motion-reversal produced by the mirror system; and Fig. 3.2.1b shows the same for tachistoscopic motion-reversal and for the control condition in which both patterns move in the same direction. It is concluded that eye movements do not contribute significant artifacts to the first 180 msecs of either kind of motion-reversal VEP.

As a further (though less conclusive) check, the horizontal electro-oculogram was monitored, and there was no indication of synchronous eye movements in the raw or the averaged EOG. Synchronous eye movements greater than about 20' would have been detectable.

3.2.2. Increased effective contrast.

It is conceivable that there might be a slight increase in

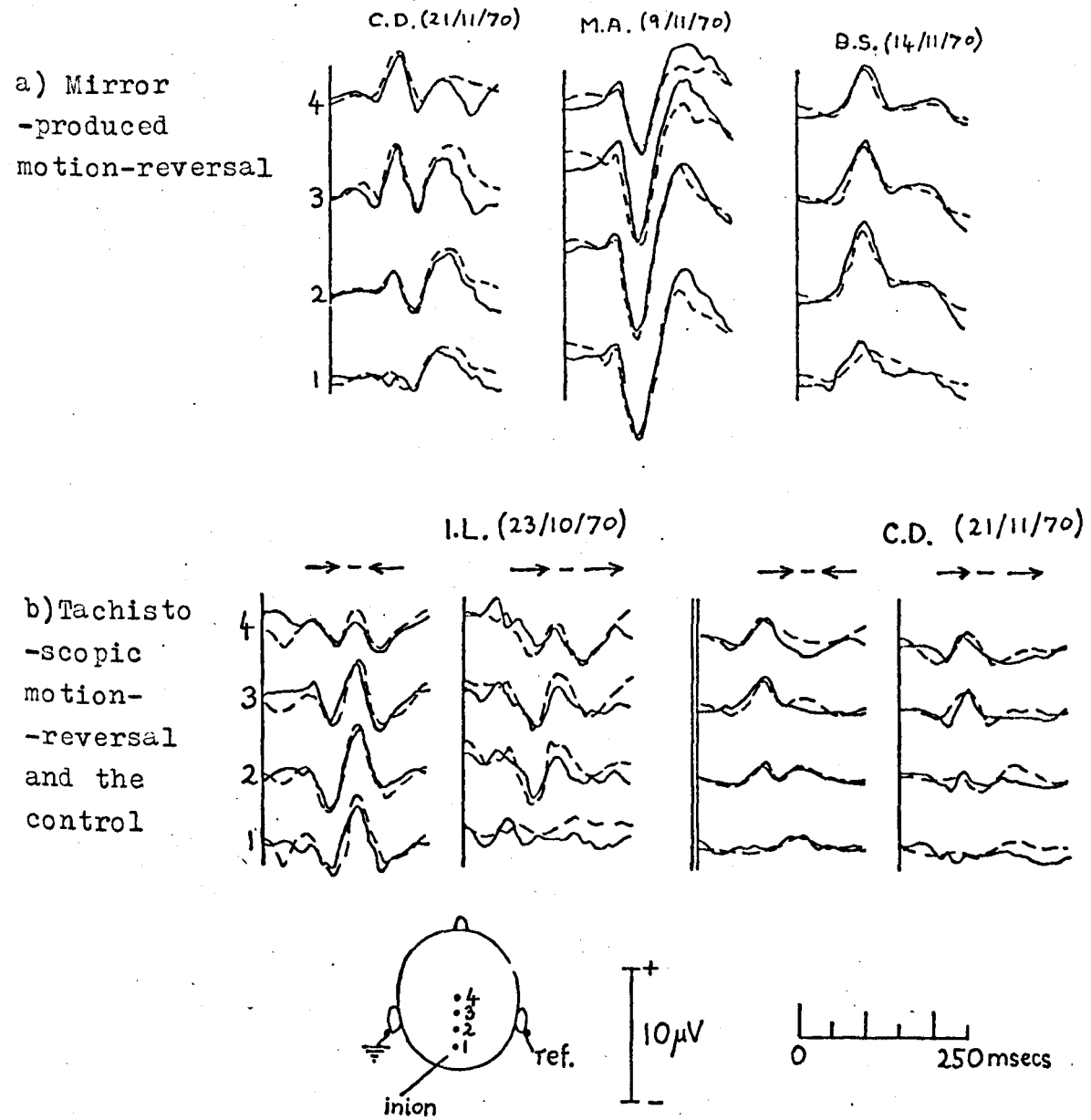


Fig. 3.2.1. Comparison of the VEPs with periodic (continuous line) and aperiodic (discontinuous line) stimulation. Electrode spacing = 3½cm. Pattern velocity = 10°/sec. Each trace is the mean of 200 responses. The standard deviation between averaged responses was about 0.5 V in each subject.

effective contrast at the moment of reversal even with an idealised stimulus, since each element of the pattern then returns over the same retinal area which it has just crossed. This is unlikely, however, since there is no corresponding subjective effect; and the VEP was insensitive to the time-course of reversal but very sensitive to the steady velocity before and after reversal (section 3.1). Even so, some experiments have been performed to investigate the possibility further.

If such contrast enhancement did occur, one would expect a similar effect due to a small step-displacement against the motion, with no reversal taking place; but not so for a step-displacement in the same direction as the motion. Fig. 3.2.2 shows that small steps in the two directions gave VEPs that were very similar, though not identical. This suggests that if there were any VEP components due to contrast enhancement, they were not large.

This conclusion is supported by another experiment. Any enhancement of contrast would be due to the increased time of stimulation of contrast-sensitive mechanisms. At most, this time of stimulation would be doubled by reversal. If that produced significant contrast enhancement, one would expect a similar effect due to suddenly halving the velocity, so the VEP to suddenly halving the velocity should contain components due to the postulated contrast enhancement as well as any motion-related components. Fig. 3.2.3a shows that, in fact, reducing velocity from 10°/sec to 5°/sec gave a very small response, especially in the first 150 msecs after the stimulus. This suggests that the hypothesized doubling of the time of stimulation of contrast-sensitive mechanisms

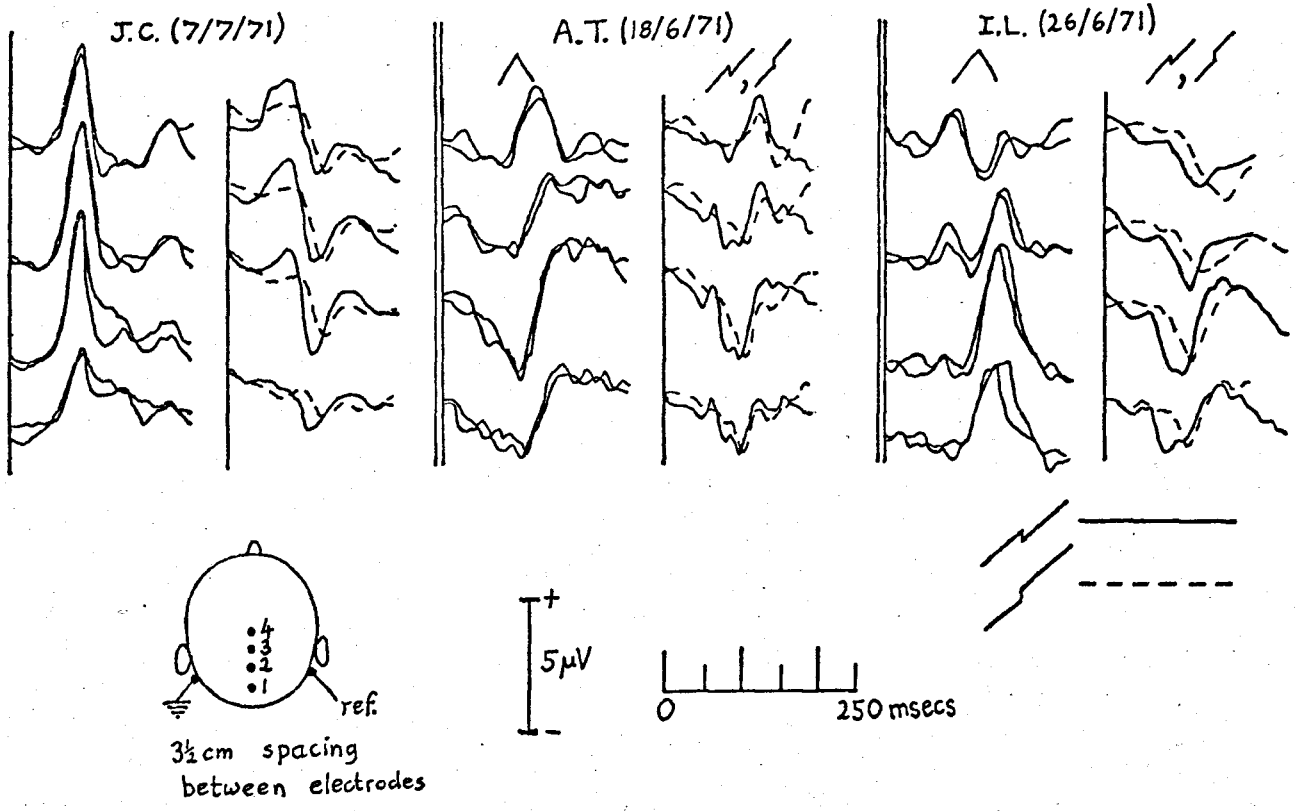


Fig.3.2.2. Comparison of the VEPs to 15' step-displacements in each of the two horizontal directions during continuous horizontal motion of the noise pattern. Motion-reversal VEPs are also shown. Velocity = 10°/sec.

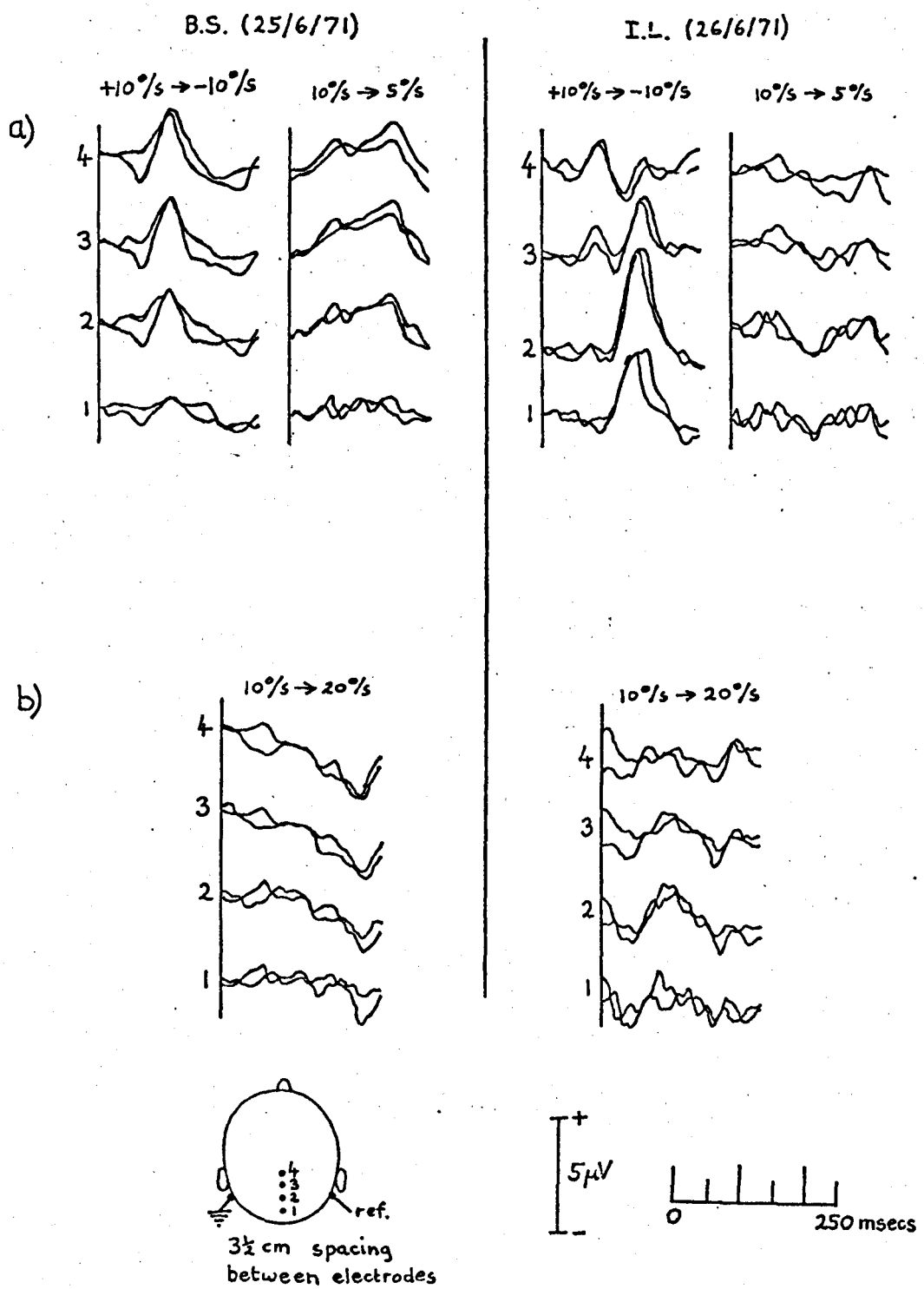


Fig. 3.2.3. Motion-reversal VEP compared with VEP to
a) halving the velocity
b) doubling the velocity

does not produce significant VEP components, and is therefore not responsible for any major components of the motion-reversal VEPs.

It should be noted, however, that a sudden large reduction in velocity (25°/sec to 5°/sec) does produce a sizeable VEP (Rietveld & MacKay, unpublished data).

3.2.3. Statistical changes in the pattern of stimulation.

The most obvious ways in which mechanisms insensitive to direction might contribute to the motion-reversal VEP have been investigated, and no indication of the activity of such mechanisms has been found. There remains, of course, the possibility that direction-insensitive mechanisms contribute by some more subtle means not considered. Two further possible sources of direction-insensitive artifact are considered below.

One danger of using an averaging method is that a statistical bias introduced by the stimulus may cause a significant and repeatable component of the averaged response. It might be thought that such an artifact could arise in the following way. Let the time of reversal be defined as $t = 0$. Then if the rate of change of contrast (or brightness) at any point in the field of vision before reversal is $F(t)$, the rate of change of contrast (or brightness) after reversal will be $-F(-t)$. Thus, at the moment of reversal there will be a 180° change of phase of all the Fourier components. It might be argued in terms of linear analysis that this could produce a contribution to the averaged VEP, but it should be remembered that the phase at reversal will vary from point to point in the visual field, and for aperiodic stimulation or imperfect fixation

it will vary from one motion-reversal to the next. So such an artifact is virtually impossible.

One further possible source of motion-insensitive artifact was investigated. Consider a population of neural mechanisms with receptive fields of width x. If the stimulus velocity is V, then the time for which any stimulus feature lies within a particular receptive field is always $\frac{x}{V}$. But if motion-reversal occurs when a particular stimulus feature lies within the receptive field, the time of stimulation can be any value between 0 and $\frac{2x}{V}$ with equal probability. Thus, following the moment of reversal there will be a change in the probability distribution of stimulation durations for the receptive fields (although the average stimulation duration will not be affected). For half the receptive fields the duration of stimulation will be increased, for the other half decreased. And these changes could in theory evoke components in the motion-reversal VEPs.

First, consider the possible effects of the increases in stimulation duration following motion-reversal. Such will occur for no more than half the receptive fields, and in no case will the increase be more than twofold. Now suddenly halving the velocity will fully double the stimulation duration for every receptive field. Hence, the VEP produced by the increases in stimulation duration following motion reversal should be considerably less, and on a linear model less than half, that produced by such increases after halving the velocity, though there may be additional motion-related components in the latter. But halving the velocity from 10°/sec to 5°/sec produces only a very small VEP, which

suggests, on the basis of the simple model above, that the effects of increased stimulation duration following motion-reversal are negligible.

Now consider the receptive fields (no more than half) whose duration of stimulation is decreased following motion-reversal. The average decrease will be by a factor of two. The effect of this should therefore be considerably less than the effect of the decreases of stimulation duration that result from doubling the velocity. But it was found that doubling the velocity from 10°/sec to 20°/sec produced only a very small VEP (Fig. 3.2.3b), which suggests that decreases of stimulation duration following motion-reversal produces negligible VEP.

The above theorizing is certainly only approximate and over-simplified, but precise analysis is not possible, in the present state of knowledge. Also, by no means all the possible ways in which direction-insensitive VEP mechanisms might be activated by instantaneous motion-reversal have been investigated. One of such is discussed in sub-section 5.2.3.

3.3. Chapter conclusion.

Adaptation experiments have shown that direction-selective processes contribute to the motion-reversal VEPs.

VEPs to reversal of movement were insensitive to variations of the turn-round time, but sensitive to the steady velocity before and after reversal. Also, VEPs to the appearance at constant luminance of stationary and of moving patterns were virtually identical for pattern-appearance durations of 10 msecs or less, and a 5 msec standstill during continuous motion produced a very small VEP. These results strongly

indicate that the brief slowing down at reversal does not cause major VEP components.

A change or displacement of the pattern at approximately the moment of reversal suppresses the VEP. A psychophysical effect has been noticed which may be connected with this.

Involuntary ~~saccadic~~ eye movements are not apparently implicated in production of the VEPs, since periodic and aperiodic stimulation yield similar results. Certain other ways in which VEP components might have arisen from direction-insensitive mechanisms even with an idealized stimulus motion have been investigated, with no indication of the occurrence of such components.

The evidence presented in this chapter indicates that motion-reversal VEPs may arise almost entirely from direction-selective mechanisms, responding by virtue of their direction-selectivity.

CHAPTER 4

(Results 2)

The characteristics of visual motion-evoked potentials

4.1. Analysis of VEPs into different components.

This work has not been restricted purely to motion-reversal VEPs; motion-onset and -offset VEPs have also been studied. And all these VEPs have been compared with those to pattern-appearance and -disappearance.

Now Jeffreys (1971) has shown that pattern-appearance VEPs contain several components of different latencies, each component normally being manifested by a peak in the voltage-time waveform. The different components often have different distributions over the scalp.

In this study, attempts have been made to analyse similarly all the different kinds of VEP under investigation, and the results are reported in this section.

4.1.1. Motion-reversal VEPs.

Motion-reversal VEPs included three main component peaks, C1, C2, C3, but not all of these were necessarily detectable for any one subject. The peak latencies were approximately 100 msecs, 120 msecs and 170 msecs. For lower half-field stimulation, C1 and C3 were positive and C2 was negative, but for upper half-field stimulation the peaks usually reversed their polarity (Figs. 4.1.8 - 4.1.9). In this respect the motion-reversal VEPs were similar to pattern-appearance VEPs (Jeffreys, 1969, 1970b, 1971) and checkerboard contrast-reversal VEPs (Halliday & Michael, 1970). Motion-reversal VEPs were recorded from the lower half-field for 38 subjects, and from the upper half-field

for 11 subjects, and only one anomalous subject has been found; it may be significant that this subject was about nine years old, whereas almost all the others were adults.

Figs. 3.1.8, 3.1.9, 4.1.1 show that the optimal velocity for production of C1 was about 20°/sec but the later peaks were largest for a much lower stimulus velocity, typically about 5°/sec. It can also be seen from the same Figs. (3.1.8, 3.1.9, 4.1.1) that, for lower half-field stimulation, C1 was usually largest at electrodes anterior to those for which the later peaks were largest. No differences between C2 and C3 in distribution along the midline was noticed, but very slight differences in the lateral distributions of these components did sometimes appear.

In one subject for whom C1 and C3 were pronounced but not C2, it was found that C3 was produced almost entirely through stimulation of the central 3° of vision whereas a large proportion of C1 was produced through stimulation outside the central region (Fig. 4.1.2). The 10° field radius used on this occasion was larger than usual. (Normally, a 4° radius field was used, for comparison with tachistoscopic VEPs, as the tachistoscope was limited to 4° radius.) The occurence of a large early component from outside the central 3°$_{\times}$ contrasts with the report of Rietveld et. al. (1967) that the pattern-related component of VEPs to flash-illumination of a checkerboard is restricted to an inner 2° radius disc. But Jeffreys (personal communication) has found that the first component of pattern-appearance VEPs includes a large contribution from beyond the central 3° of vision.

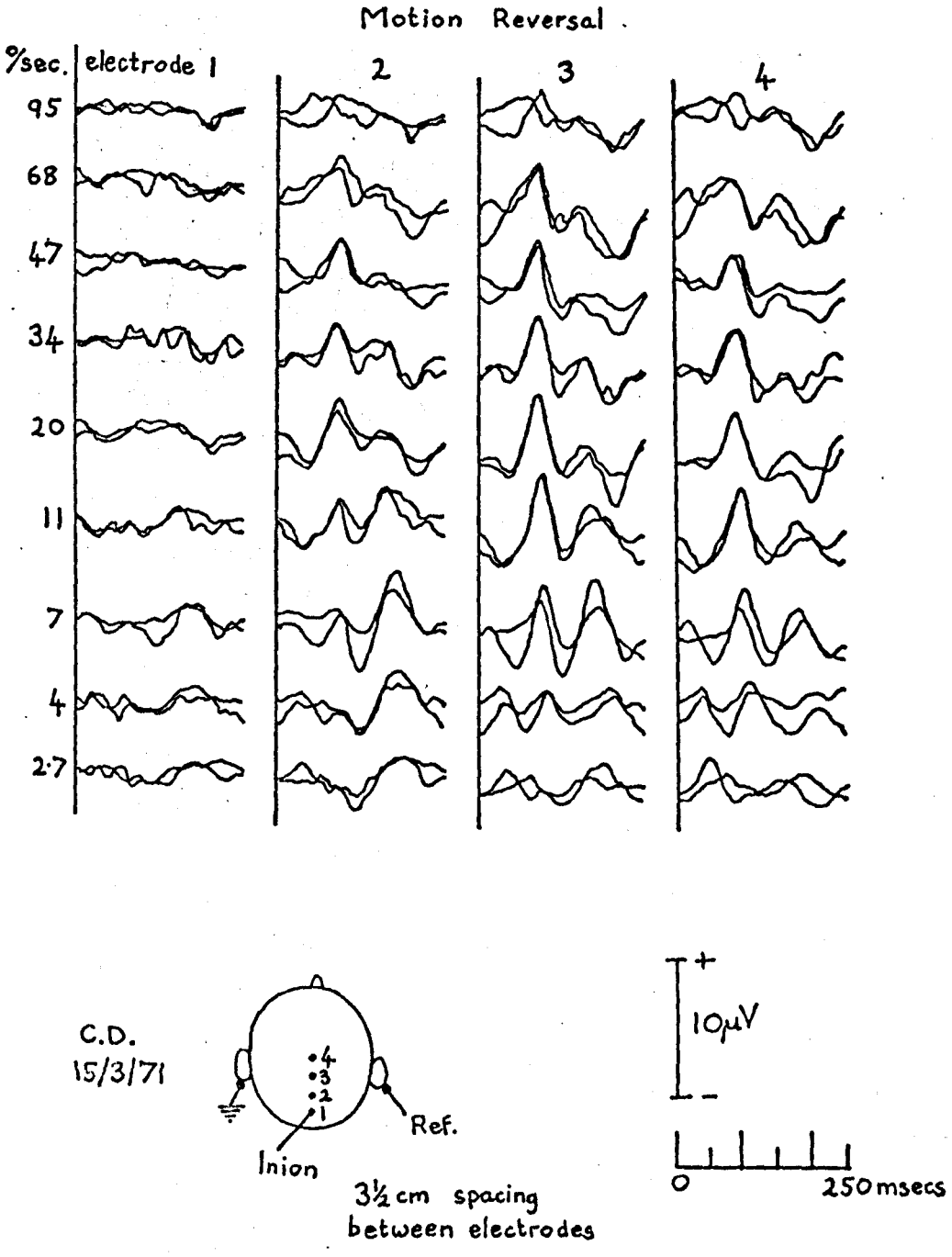


Fig.4.1.1. The effect on the motion-reversal VEPs of variations in the velocity. (See also Figs 3.1.8-3.1.9).

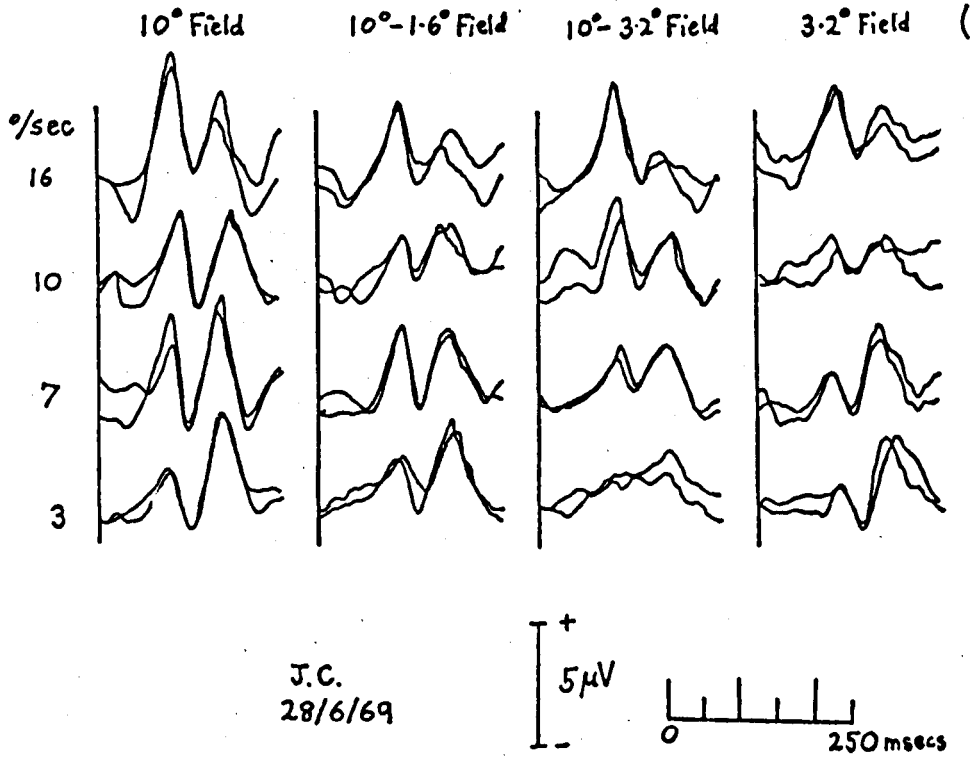


Fig.4.1.2. The effects on the motion-reversal VEPs of variations in the velocity and the retinal area stimulated.

Blocking the central retinal area selectively diminishes the third VEP component, leaving the first component relatively unaffected. In this subject the second (negative) component is too small to be measured.

The first component is largest for high velocities, but the third is largest for lower velocities. (see Figs 3.1.8, 3.1.9, 4.1.1).

4.1.2. Motion-offset VEPs.

Motion-offset VEPs were studied much less extensively than motion-reversal VEPs, in a total of 12 subjects. The VEPs to offset were similar to the reversal VEPs in that they comprised three main components (C1, C2, C3), of which C1 and C3 were positive and C2 was negative for lower half-field stimulation. Stimulating the upper, instead of the lower, half-field usually reversed the polarity of the components of offset VEPs just as it did for reversal VEPs (Figs. 4.1.8 - 4.1.9) and in the same subjects. The latencies of the components were slightly longer: approximately 110 msecs for C1, 130 msecs for C2 and 190 msecs for C3.

Figs. 4.1.3 - 4.1.5 show motion-offset VEPs for a wide range of velocities. The components had similar distributions over the scalp to the corresponding motion-reversal VEP components (C1 was located anterior to C2 and C3 which had very similar, though not quite identical, distributions); and, as for motion-reversal, the optimal velocity for production of the first peak was greater than that for which the later peaks were largest. But the motion-offset VEP components were larger than those to reversal, and the optimal velocity for producing them was larger (c 50°/sec for the first, and 15°/sec for the later ones).

As discussed in chapter 1, motion-offset is inherently more likely than motion-reversal to evoke a response from the mechanisms which produce pattern-appearance VEPs. Such a response may well have contributed to C1, since this component was large even for the highest velocities, though it was normally reduced slightly for increases to above about 50°/sec.

Figs 4.1.3 - 4.1.5

The effects on the motion-offset VEPs of variations in the velocity.

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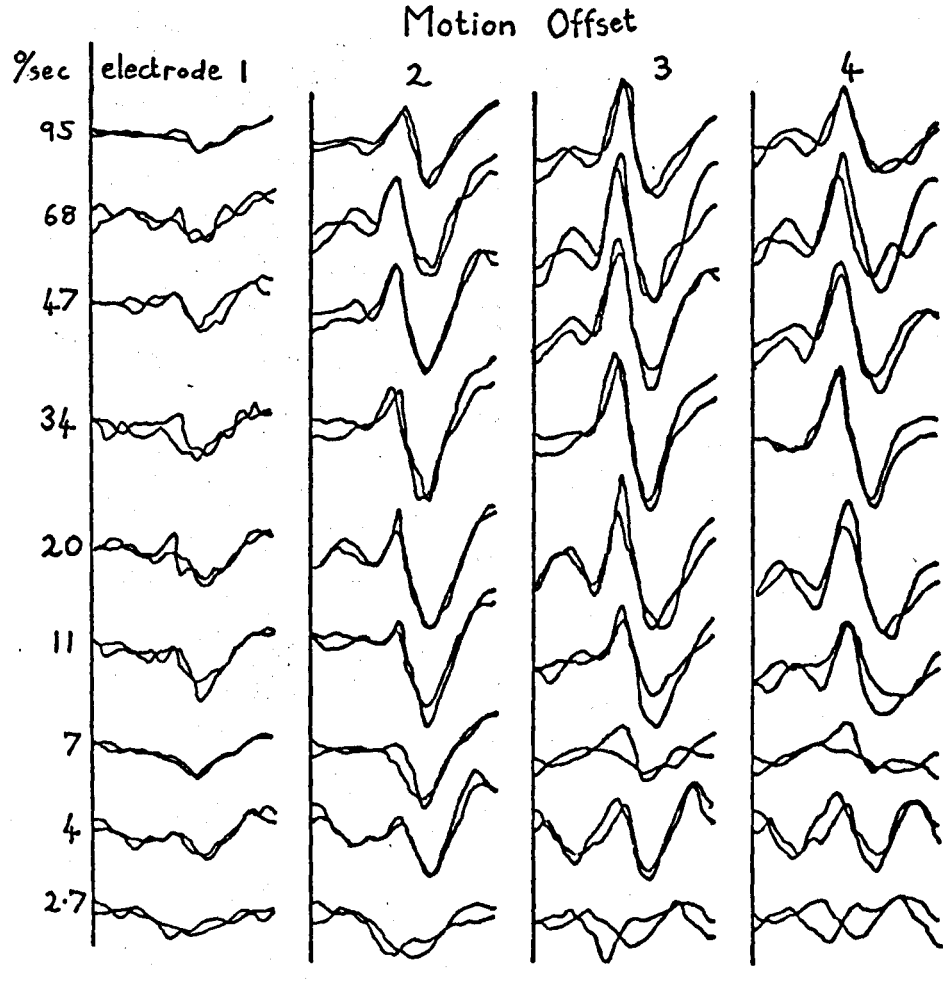
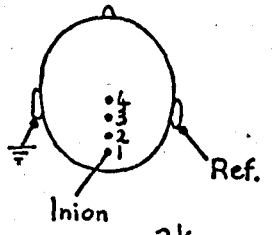


C.D.
15/3/71



3½cm spacing
between electrodes

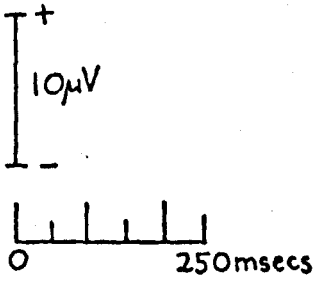
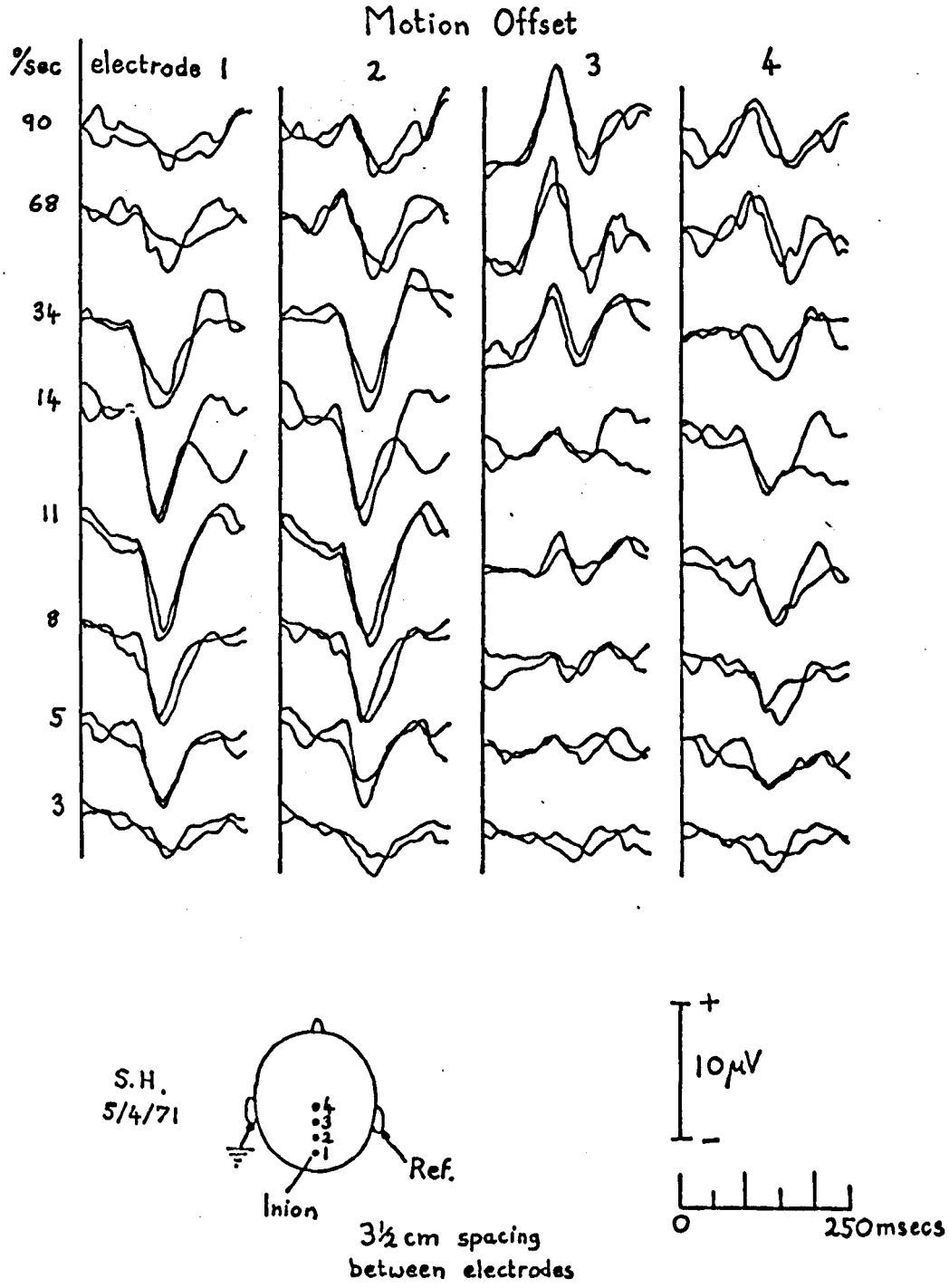


Fig. 4.1.3


Motion Offset
%sec
electrode 1
2
3
4
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68
34
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11
8
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3
S.H.
5/4/71
4
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between electrodes
+
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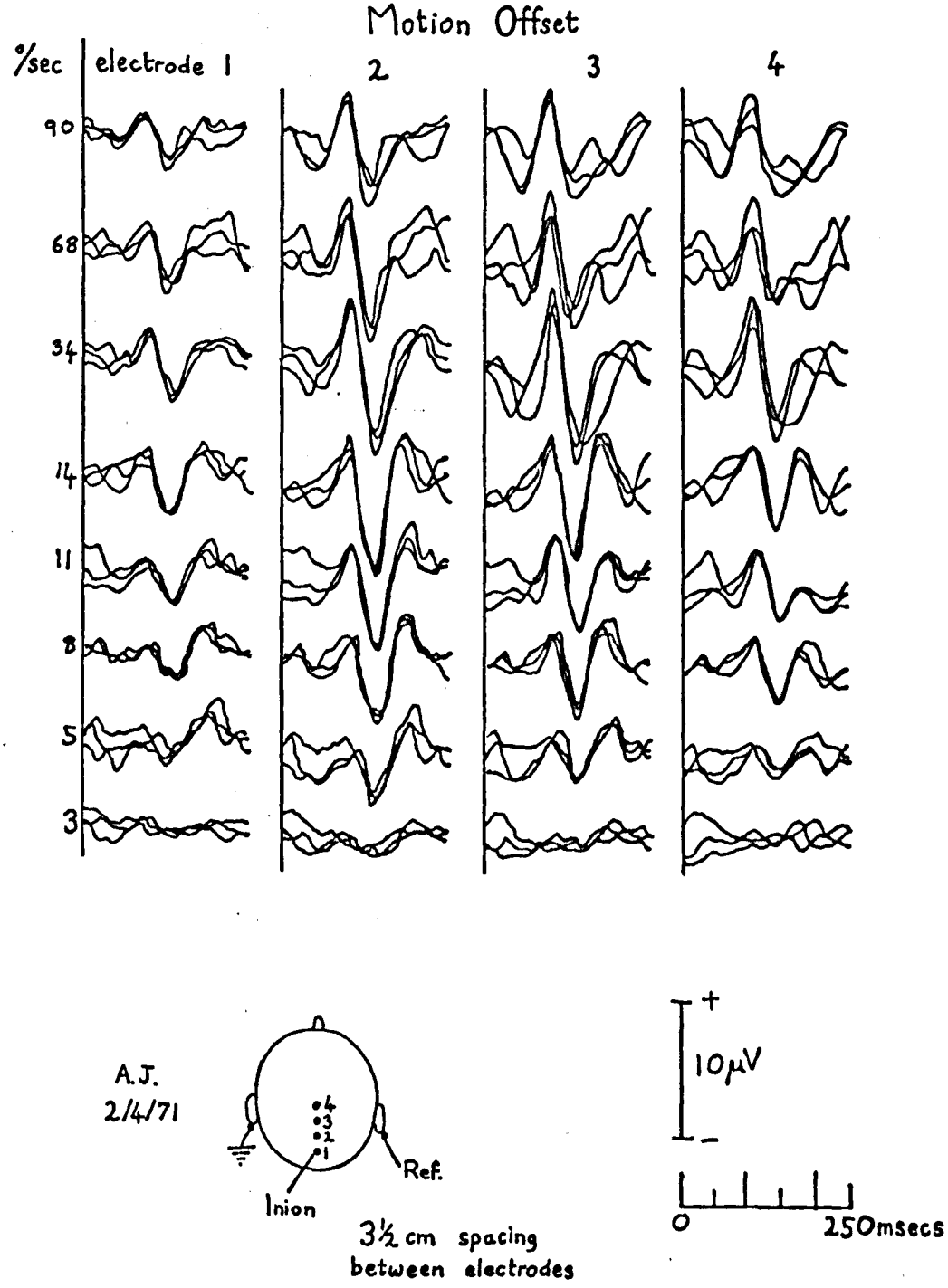
Fig. 4.1.4


Motion Offset
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3½ cm spacing
between electrodes
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250msecs

Fig.4.1.5

It is unlikely, however, that such a response contributed to the later components as these were greatly reduced, and sometimes completely abolished, at the highest velocities.

4.1.3. Motion-onset VEPs.

Motion-onset VEPs were recorded in the same 12 subjects as were the motion-offset VEPs. But responses to onset of motion were usually very small at the velocities normally used (10°/sec), so it has not been practicable to study these in great detail.

For lower half-field stimulation, if there was a measurable response it usually included a positive peak at about 140 msecs and often a later negative peak at about 190 msecs (Figs. 4.1.6 - 4.1.7). Both peaks were largest for high velocities. The late negative peak was largest at electrodes anterior on the scalp to those for which the positive peak was largest. In subject S.H. (Fig. 4.1.6) there was also a 100 msec negative peak (especially at electrode 2 for 34°/sec), but this early peak has not been observed in other subjects.

The 140 msec positive peak increased its latency to 160-170 msecs at low velocities (Figs. 4.1.6 - 4.1.7) corresponding to the latency of the late positive peak in the motion-reversal VEPs (Figs. 3.1.8 - 3.1.9), which is also large at low velocities and similarly distributed over the scalp. But, apart from this, there was usually little similarity between the VEPs to motion-onset and those to motion-reversal and -offset. There was, however, some evidence that the VEPs to motion-reversal were a combination of the separate VEPs to motion-onset and offset. If that is so, the apparent lack of similarity between the VEPs to motion-onset and

Figs 4.1.6 - 4.1.7

The effects on the motion-onset VEPs of variations in the velocity.

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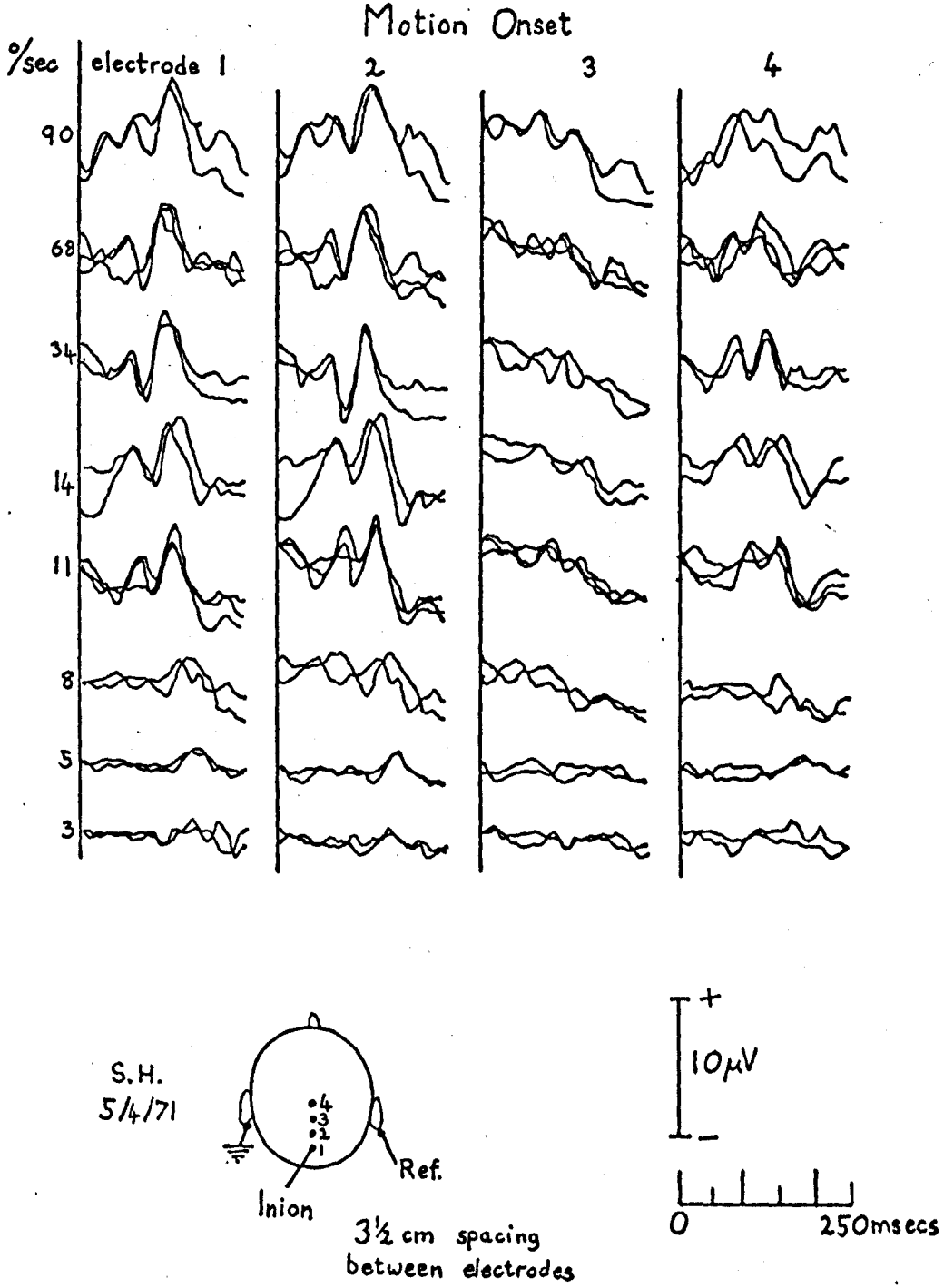
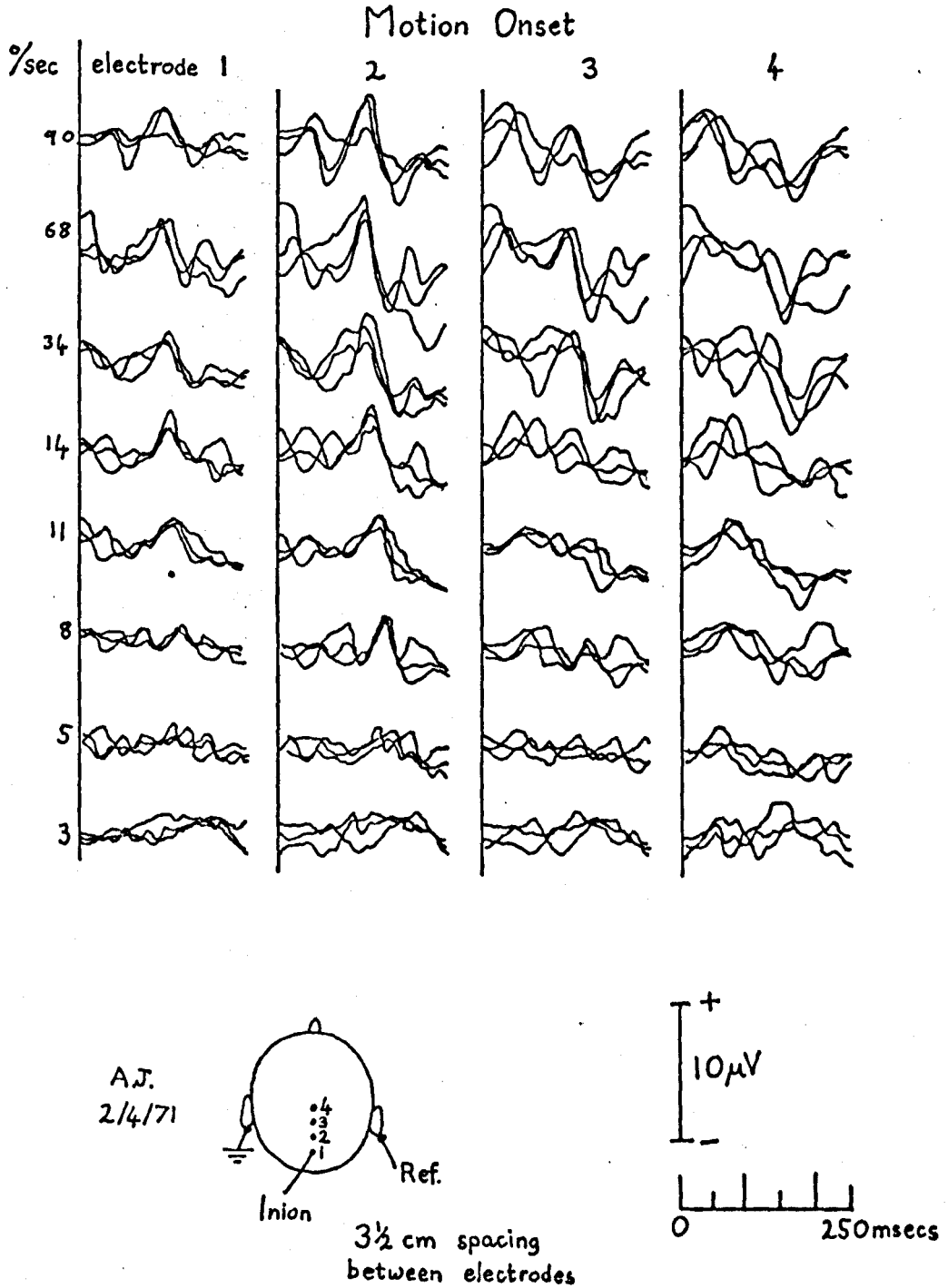

Motion Onset
°/sec
electrode 1
2
3
4
90
68
34
14
11
8
5
3
S.H.
5/4/71
4
3
2
1
Ref.
Inion
3½ cm spacing
between electrodes
+
10μV
−
0
250msecs

Fig. 4.1.6


Motion Onset
%sec
electrode 1
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A.J.
2/4/71
4
3
2
1
Ref.
Inion
3½ cm spacing
between electrodes
+
10μV
−
0
250msecs

Fig. 4.1.7

-reversal is probably due to the predominance of the motion-offset VEP compared with the -onset VEP.

4.1.4. How the above VEPs relate to each other and to pattern-appearance and - disappearance VEPs.

(a) Motion-reversal and - offset VEPs, and pattern-appearance VEPs.

Evidence will now be presented that C1 of the VEPs to motion-reversal and -offset arose in the same area of cortex as C1 of the pattern-appearance VEPs, namely striate cortex (Jeffreys, 1971); and that C2 and C3 of the motion-reversal and - offset VEPs arose in the same area or areas of cortex as C2 and C3 of the pattern-appearance VEPs, probably extra-striate cortex.

The main evidence for this is based on the relative distributions of the different VEP components. In all subjects, for both upper and lower half-field stimulation, the C1's of all three kinds of VEP (motion-reversal and -offset, and pattern-appearance) had indistinguishable distributions. Similarly the C2's and the C3's. The distributions of C2 and C3 were quite similar, but in some cases there seemed to be slight differences. The distribution of C1 was usually distinctly different from that of C2 and C3.

For example, in subject M.S. (Figs. 4.1.8 - 4.1.9) all three kinds of VEP contained three main component peaks, each of which exhibited polarity reversal between upper and lower half-field stimulation. In all three VEPs C1 was positive, and largest at electrode 5, for lower half-field stimulation; and negative, and largest at about electrode 1 or 2, for the upper half-field. In all three VEPs C2 was negative and largest

Figs 4.1.8 - 4.1.9

Motion-reversal and -offset VEPs and pattern-appearance VEPs for lower (Fig.4.1.8) and upper (Fig.4.1.9) half-field stimulation.

For motion-reversal and -offset, velocity = 10°/sec. The duration of pattern-appearance was 40msecs.

For this subject, all three components of all three kinds of VEP exhibited polarity reversal between conditions of lower and upper half-field stimulation. Components of the three kinds of VEP which roughly corresponded in latency and polarity, also corresponded in distribution over the scalp. This was true for both lower and upper half-field stimulation.

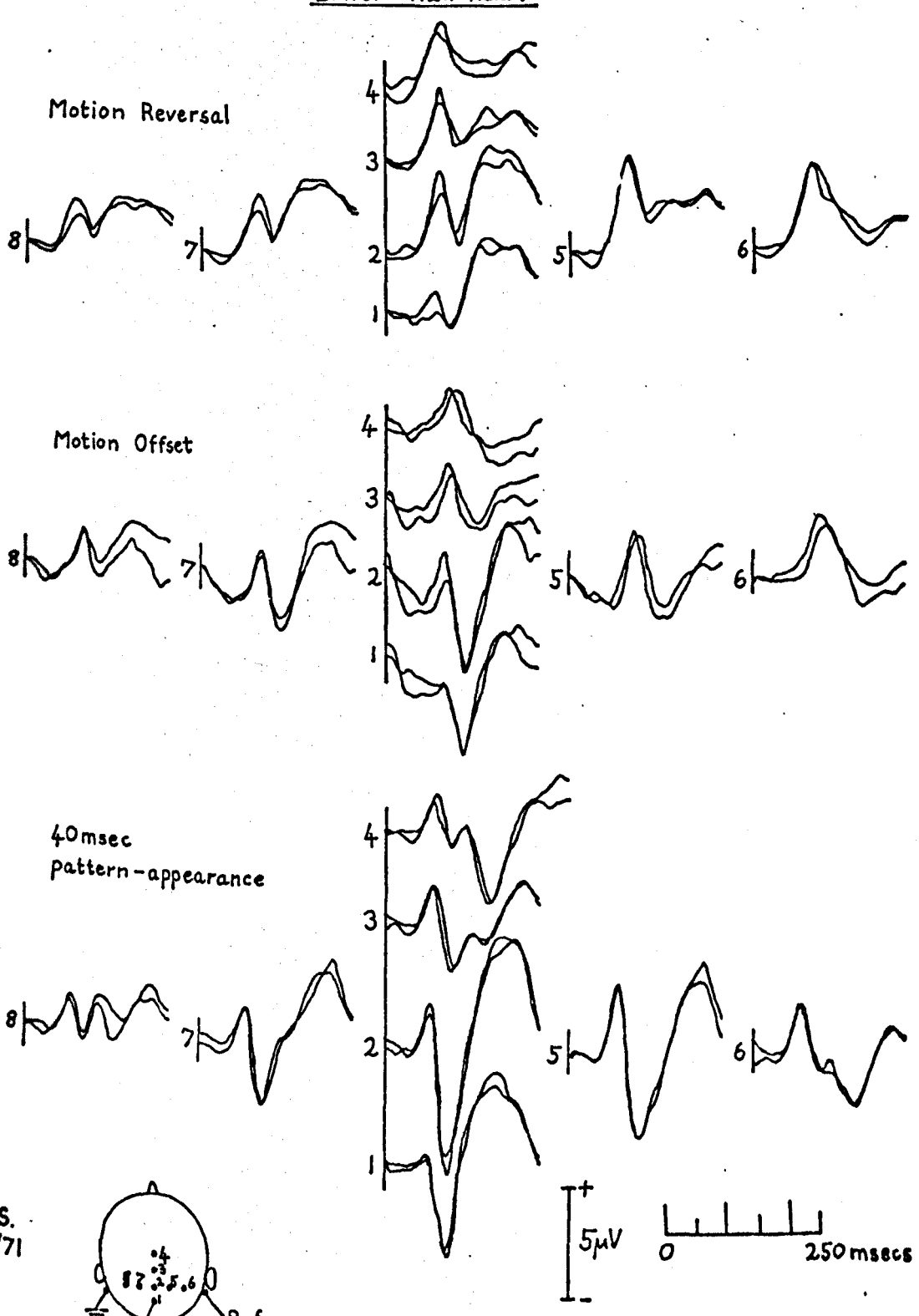
Lower Half-field.
Motion Reversal
Motion Offset
40msec
pattern-appearance
8
7
4
3
2
1
5
6
+
5μV
−
0
250msecs
M.S.
7/4/71
Inion
Ref.
3½ cm spacing
between electrodes

Fig. 4.1.8

Upper Half-field.

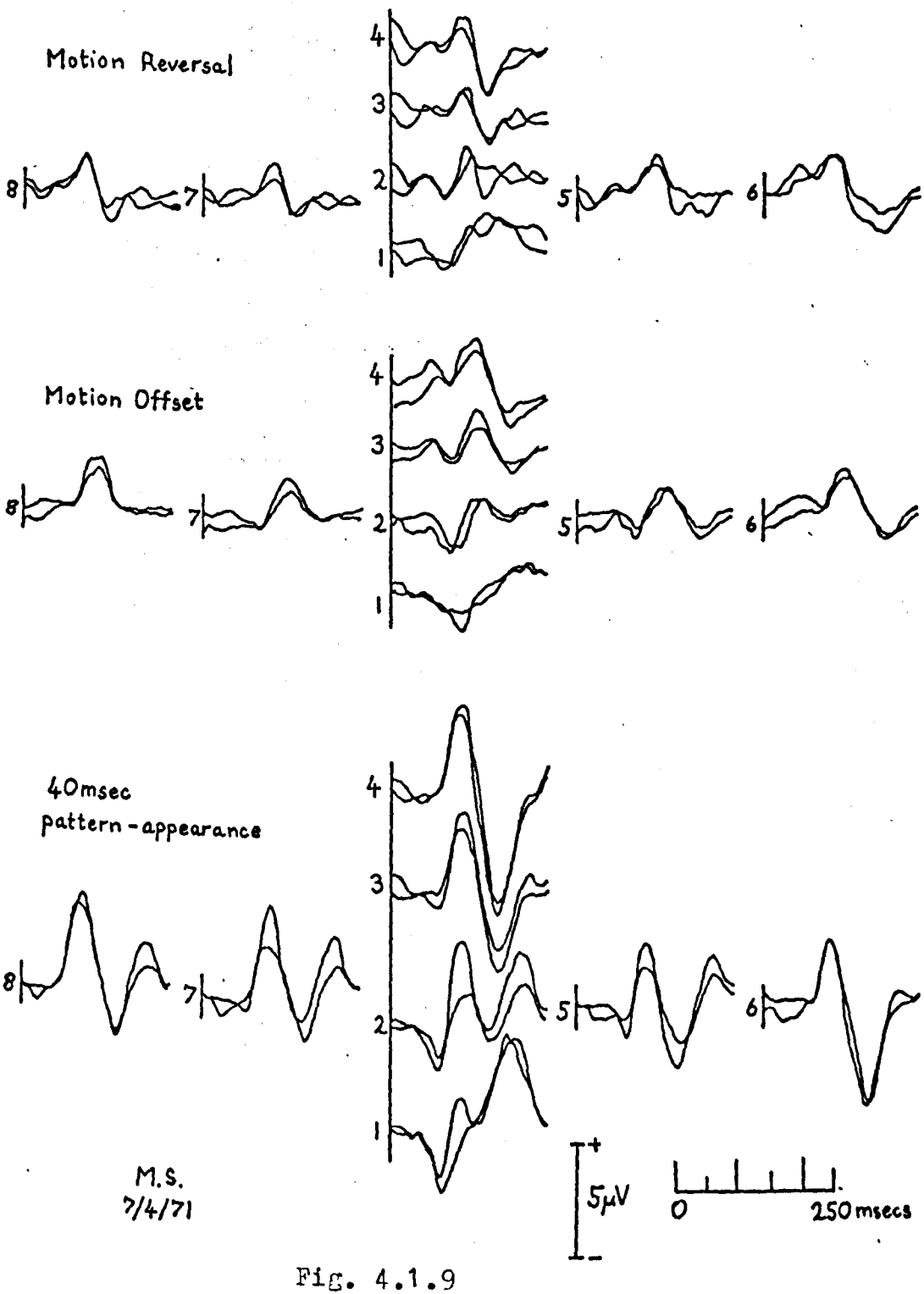

Fig. 4.1.9

at electrode 2 (lower half-field); or positive and largest at electrodes 4, 6 and 8 (upper half-field). C3 was of opposite polarity to C2 and similarly distributed, except that for upper half-field stimulation it was small at electrodes 7 and 8, where C2 was comparatively large. The pattern-appearance VEP was always larger than the others, however.

The fact that the n^{th} ($n = 1, 2, 3$) components of the three kinds of VEP had similar distributions over the scalp and sensitivities to change of retinal area suggests that the underlying neural mechanisms were similarly located. Slight differences in distribution between C2 and C3 suggest that the locations of the underlying mechanisms, although similar, were probably not identical.

Now the careful work of Jeffreys (1970b, 1971, and unpublished data) indicates that in pattern-appearance VEPs, C1 originates in striate cortex, and C2 in extrastriate (see sub-section 1.1.4). It would seem, therefore, that C1 of both the motion-reversal and - offset VEPs originates in striate cortex, C2 and C3 in extrastriate cortex.

Now it is likely that variability in the topography of the cortex (Polyak, 1957) is one of the main causes of inter-individual differences in VEPs (Jeffreys, 1971), so if the postulated similarities in spatial location exist, one would expect there to be positive correlations between the amplitudes of the corresponding components of the different kinds of VEP for different subjects.

This was tested for 13 subjects, comparing pattern-appearance (40 msec exposure) VEPs with 10°/sec motion-reversal VEPs. Motion-offset VEPs were not studied in this test.

Peak amplitudes were measured from the baseline. Overlapping of components was probably not great at the peaks, but its existence cannot be neglected. The standard deviation of the averaged VEPs (200 samples or more) was usually less than 0.5μV.

Table 4.1.1 shows that there was indeed a significant ($p<0.025$) positive correlation between the amplitudes (A1, A2, A3) of each of the pairs of component peaks (C1, C2, C3) of the two kinds of VEP (Figs. 4.1.10 – 4.1.12); also between A2 and A3 for motion-reversal, and between A2 for motion-reversal and A3 for pattern-appearance. Nearly significant correlations existed between A2 for pattern-appearance and A3 for both motion-reversal and pattern-appearance. There was no evidence, however, of even weak correlation between A1 of either VEP and the amplitude of any later component.

There appears then to be correlation between A2 and A3 of the two kinds of VEP (in all combinations) and also between the A1's; but not between A1 and the later component amplitudes. This supports the previous conclusion that the similarities of scalp distribution of the first components on the one hand, and the later components on the other, reflect similarities in location of the underlying mechanisms. The fact that correlation between A2 or A3 of the two kinds of VEP was greater than that between A2 of one VEP and A3 of the other may correspond to the fact that there were slight differences in distribution between C2 and C3. But this apparent correspondence may be due to chance.

In fact, the main limitation of this study was the small size (13) of the sample, resulting in large standard deviations of the calculated

		motion-reversal			pattern-appearance		
		1st peak	2nd peak	3rd peak	1st peak	2nd peak	3rd peak
motion-reversal	1st peak	(1)					
	2nd peak	-0.20	(1)				
	3rd peak	-0.22	+0.83 (.49-.95)	(1)			
pattern-appearance	1st peak	+0.75 (.34-.92)	-0.31	-0.16	(1)		
	2nd peak	-0.13	+0.66 (.17-.89)	+.49	-.15	(1)	
	3rd peak	+0.01	+0.61 (.09-.87)	+0.73 (.30-.92)	-0.14	+0.52	(1)

Table 4.1.1. Correlation coefficients for the relationships between the different VEP components.

Sample size: n=13 (subjects)

Any correlation above +0.55 is significant (p=.025). 95% confidence limits are shown in brackets below correlation coefficients that are significant.

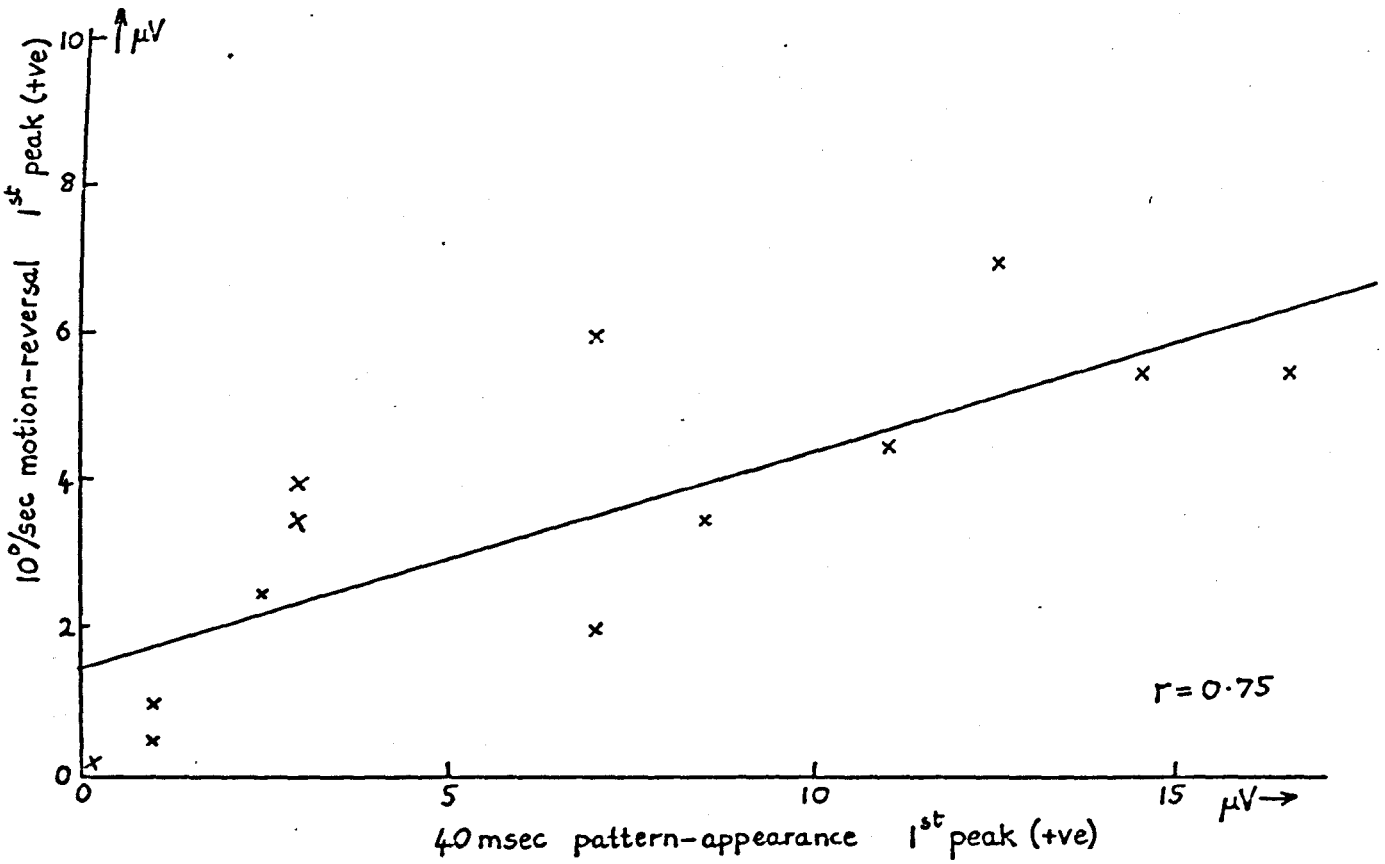

Fig.4.1.10. The amplitude of the first peak of the motion-reversal VEP plotted against the amplitude of the first peak of the pattern-appearance VEP for 13 subjects.

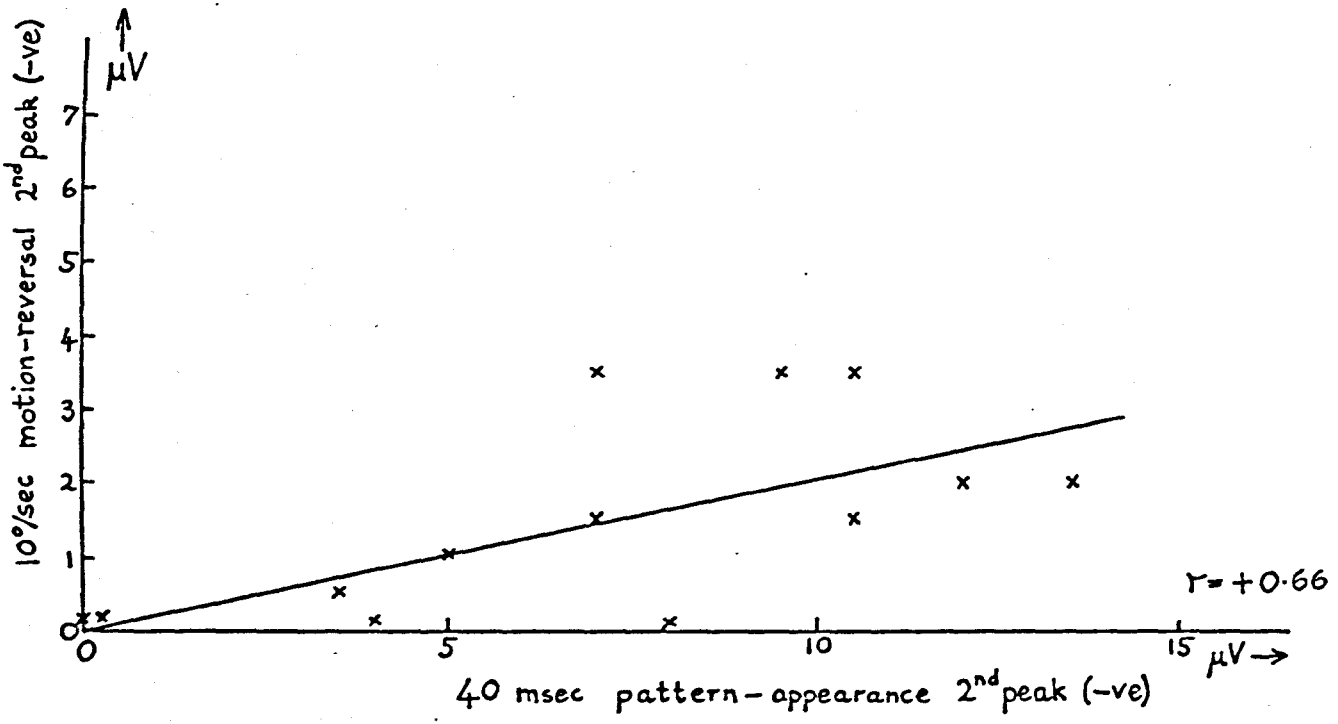

Fig.4.1.11. The amplitude of the second peak of the motion-reversal VEP plotted against the amplitude of the second peak of the pattern-appearance VEP for 13 subjects.

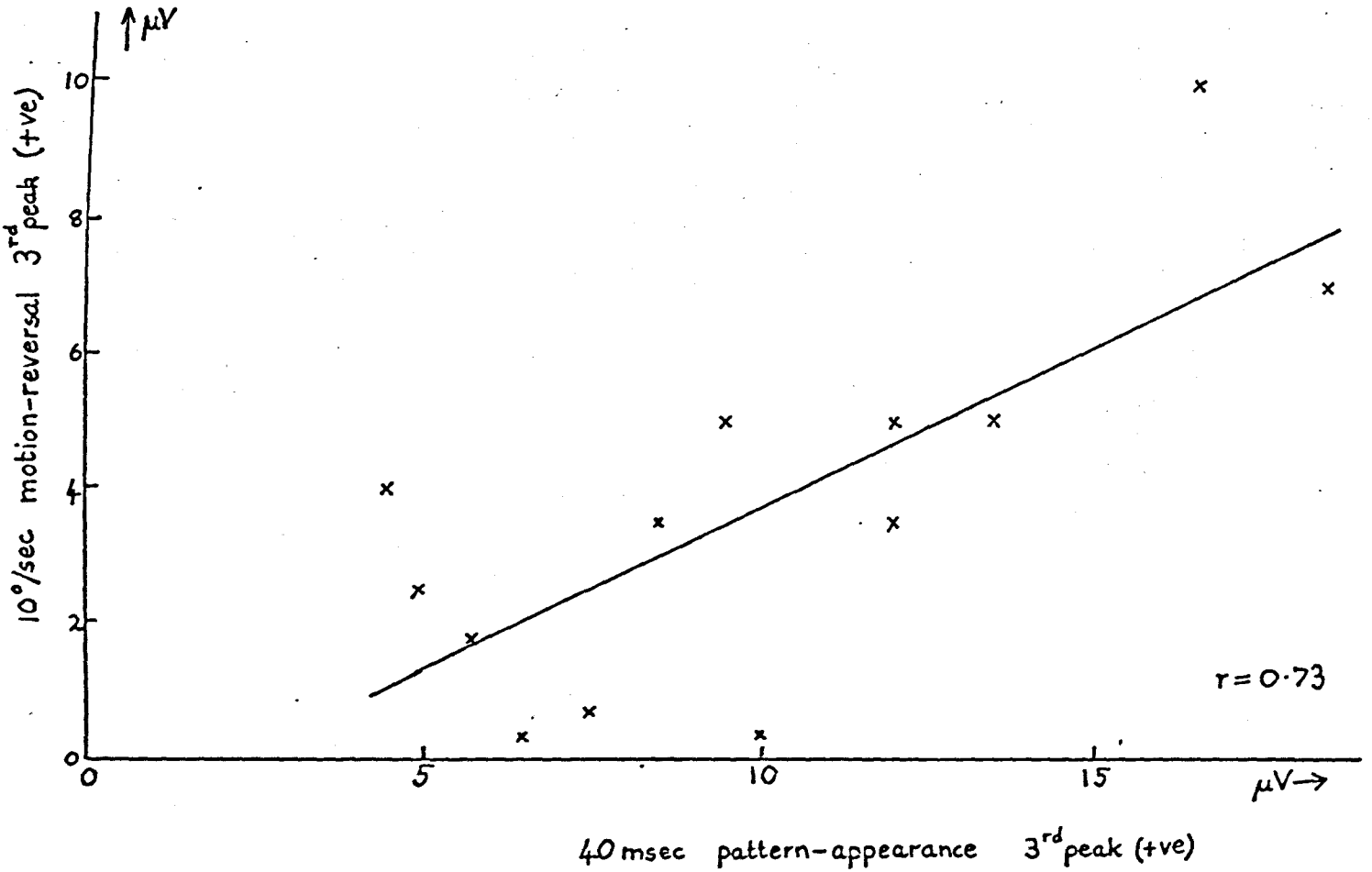

Fig.4.1.12. The amplitude of the third peak of the motion-reversal VEP plotted against the amplitude of the third peak of the pattern-appearance VEP for 13 subjects.

correlation coefficients.

The calculated correlations would presumably have been higher, however, were it not for the presence of residual noise in the averaged VEPs. Overlapping of VEP components, though not great, probably also tended to reduce the calculated correlations. Also, the third component of the pattern-appearance VEP appeared to be a composite phenomenon, probably comprising several sub-components including a pattern-~~appearance~~ disappearance VEP component, as noted also by Jeffreys (1971). This sometimes made it difficult to identify the main pattern-appearance-related third component.

(b) Motion-onset VEPs and pattern-disappearance VEPs.

It has been demonstrated that the VEPs to motion-reversal and motion-offset were similar to pattern-appearance VEPs, but motion-onset VEPs were very different. Fig. 4.1.13 illustrates a motion-onset VEP with a prominent 140 msec positive peak, compared with the VEP to pattern-disappearance, which also had a prominent 140 msec positive peak, with a very similar distribution over the scalp. The amplitude of this peak increased with velocity, and it was large even at the highest velocity used (90°/sec) (Fig. 4.1.6 - same subject ; and 4.1.7). This all suggests that the 140 msec positive peak in the motion-onset VEP, or even the whole VEP may have originated in the mechanisms responsible for pattern-disappearance VEPs; but that possibility has not been investigated in detail.

(c) VEPs to motion-onset, - offset and - reversal.

There is some evidence, however, that for medium or slow velocities (<20°/sec) the motion-onset VEP arose largely in mechanisms

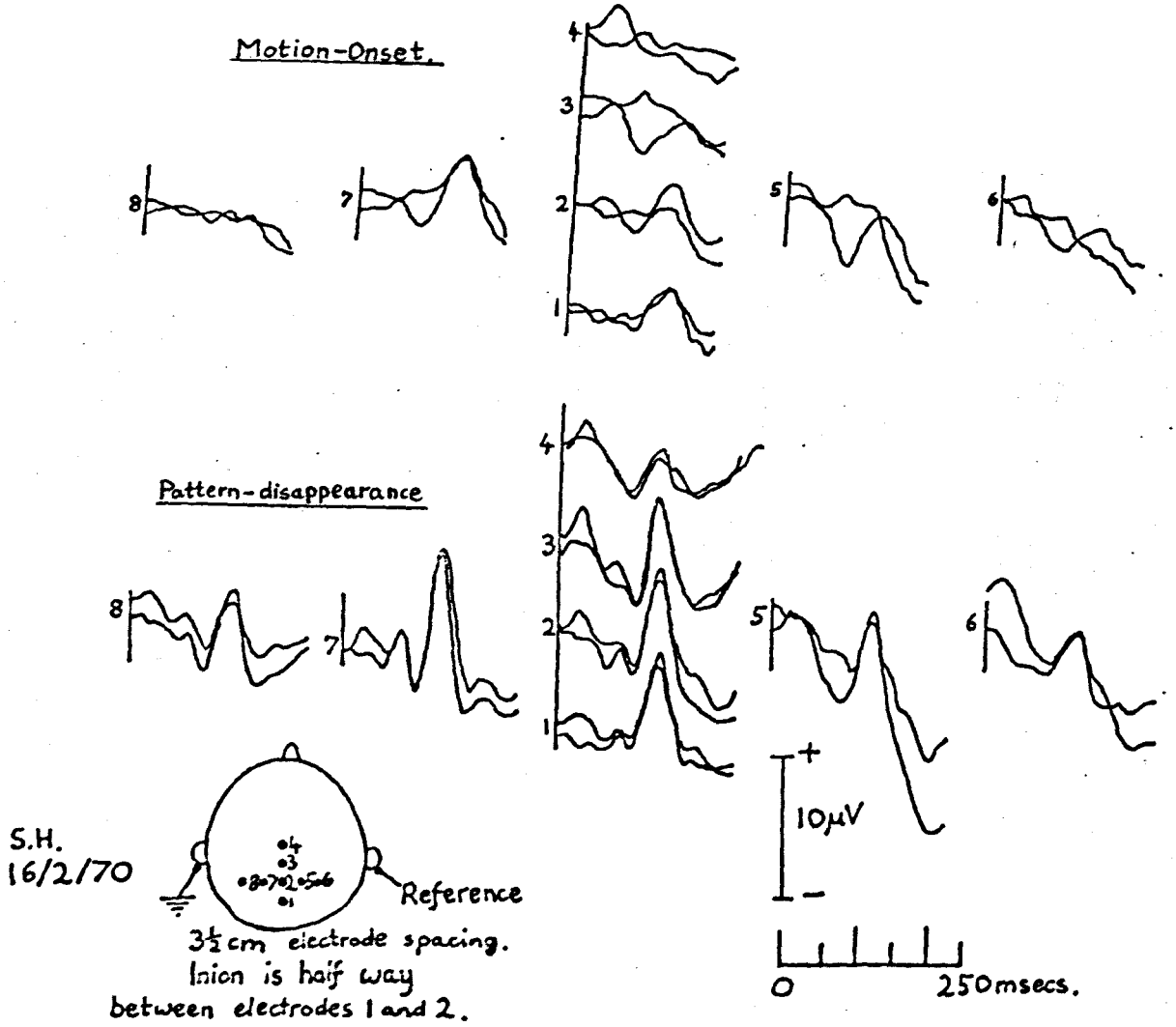

Fig.4.1.13. VEPs to motion-onset (11°/sec) and to pattern-disappearance. The pattern exposure duration was 500msecs, alternating with similar durations of blank. The two VEPs had similar waveforms and distributions, but the amplitude of the motion-onset VEP was much the smaller.

which also contributed to the motion-reversal VEPs. For, in subjects who gave a measurable VEP to motion-onset, it was usually found that components of similar latency, polarity and distribution were common to the motion-onset and motion-reversal VEPs (Figs. 4.1.14 - 4.1.15). Indeed, in such cases the motion-reversal VEP was sometimes very roughly equal to the sum of the onset and offset VEPs (same Figs. 4.1.14 - 4.1.15). Fig. 4.1.16 illustrates a case for which this was true over the velocity range 2.9 to 16°/sec; but it was not true for higher velocities (~ 90°/sec) as the motion-reversal VEPs were then very small indeed, whereas the onset and offset VEPs contained large components which did not cancel out when the VEPs were added together. Nor was it true for all subjects; and in many cases the motion-onset VEP was so small that the equation: "onset VEP + offset VEP = reversal VEP" amounted to no more than a statement of close similarity between offset and reversal VEPs, a fact that has already been noted.

4.2. The effect of varying certain parameters.

4.2.1. Brightness.

Motion-reversal VEPs were recorded for various brightness levels (Figs. 4.2.1 - 4.2.2), but were found to be not very dependent on this parameter over the range investigated (-0.7 to +1.3 log. ft. lamb). The peaks did tend to increase in latency (about 5 msec per log. unit) as the brightness was reduced, however; and at the lowest level used (-0.7 log. ft. lamb., approximately the lower limit of the photopic range), the VEPs were distinctly reduced, especially the later components. Also, there were some differences in waveform between VEPs recorded at different

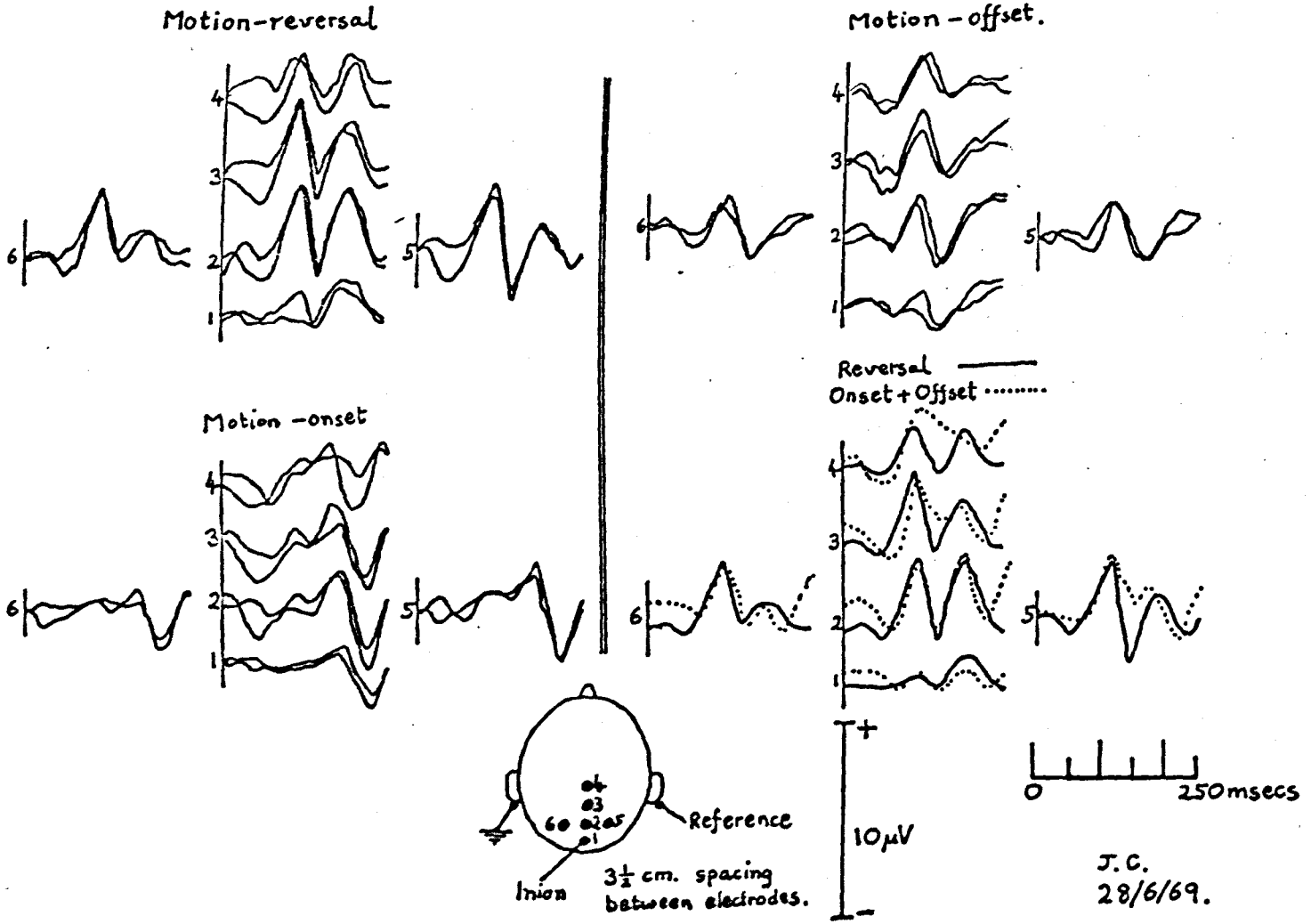

Fig.4.1.14. Comparison of the motion-reversal VEP with the motion-onset and -offset VEPs, and the sum of the latter. Velocity = 10°/sec. (See the text).

Figs 4.1.14 - 4.1.15

Motion-reversal VEPs compared with the sums of the VEPs to motion-onset and -offset.

Velocity = 11°/sec (S.H., Fig.4.1.4),
10°/sec (J.C., Fig.4.1.5).

Judging by the latencies, polarities and distributions of the components, it appears that the main components of the onset and offset VEPs are present in the reversal VEPs.

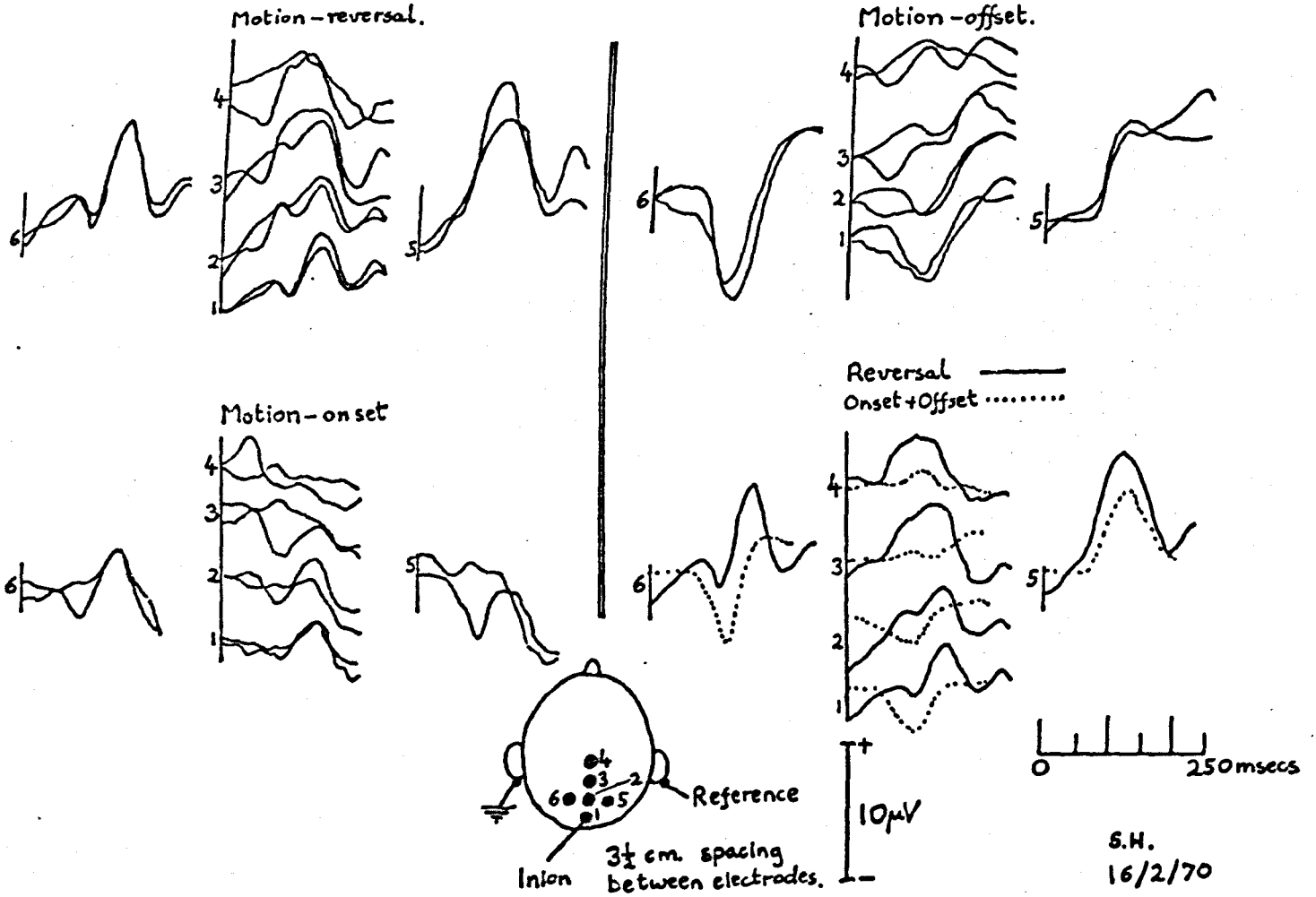

Fig.4.1.15. Comparison of the motion-reversal VEP with the motion-onset and -offset VEPs, and the sum of the latter. Velocity = 10°/sec. (See the text).

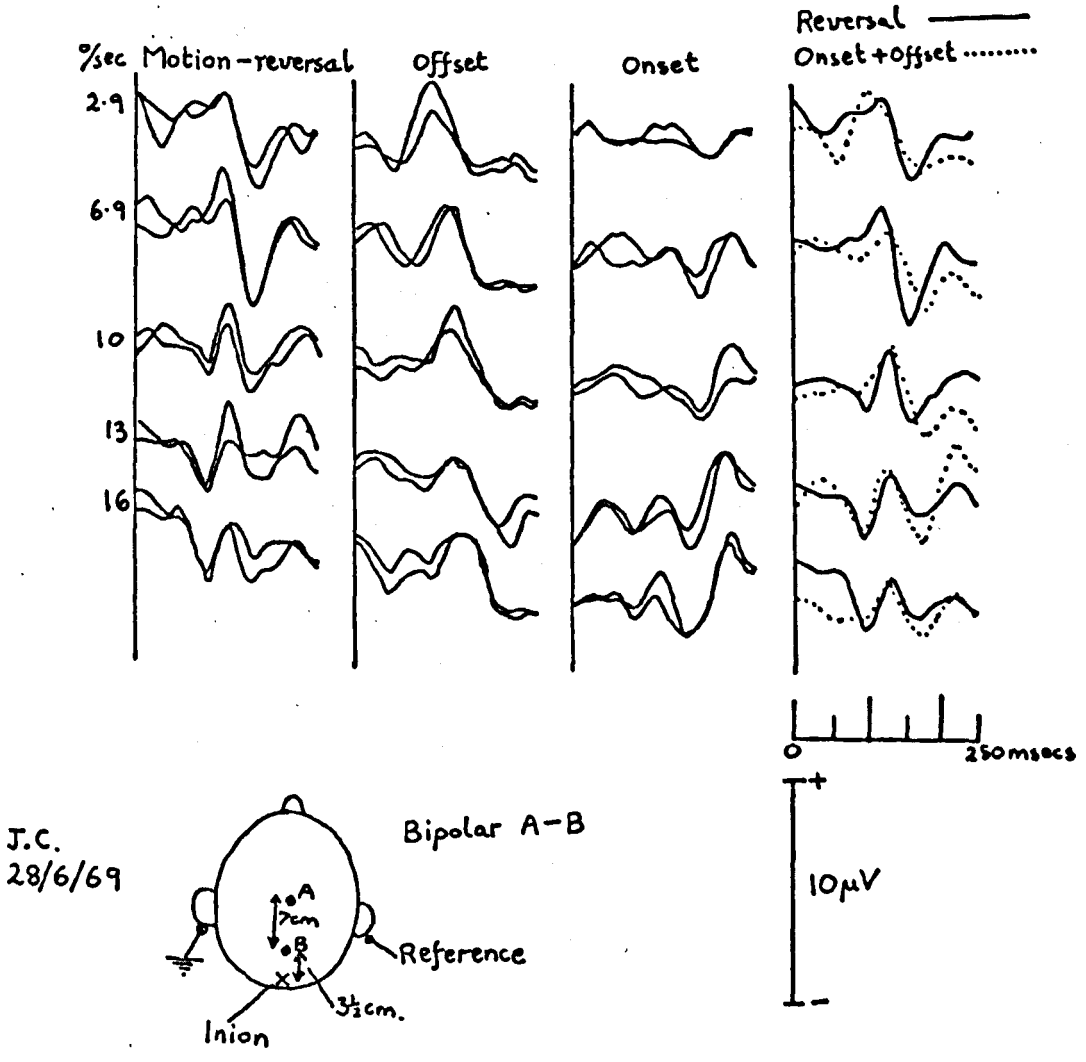

Fig.4.1.16. Motion-reversal VEP compared with motion-onset VEP + motion-offset VEP for various velocities.

The main components of the onset and the offset VEPs appear to be present in the reversal VEP for all velocities within the range investigated.

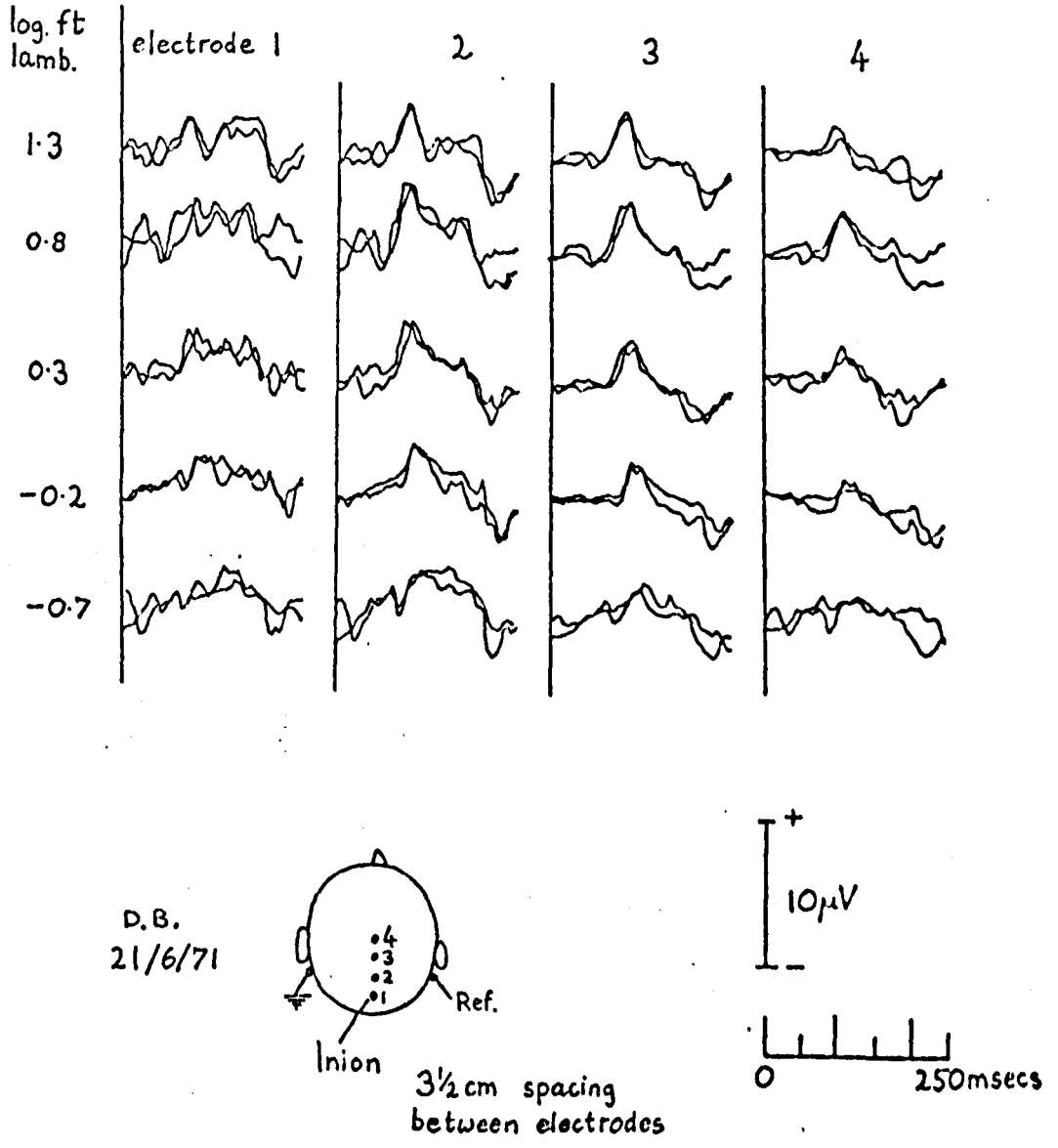

Fig.4.2.1. The effect on the motion-reversal VEP of varying the pattern brightness. (Velocity = 10°/sec.) Changes in brightness do not greatly affect the VEPs except at very low brightness level.

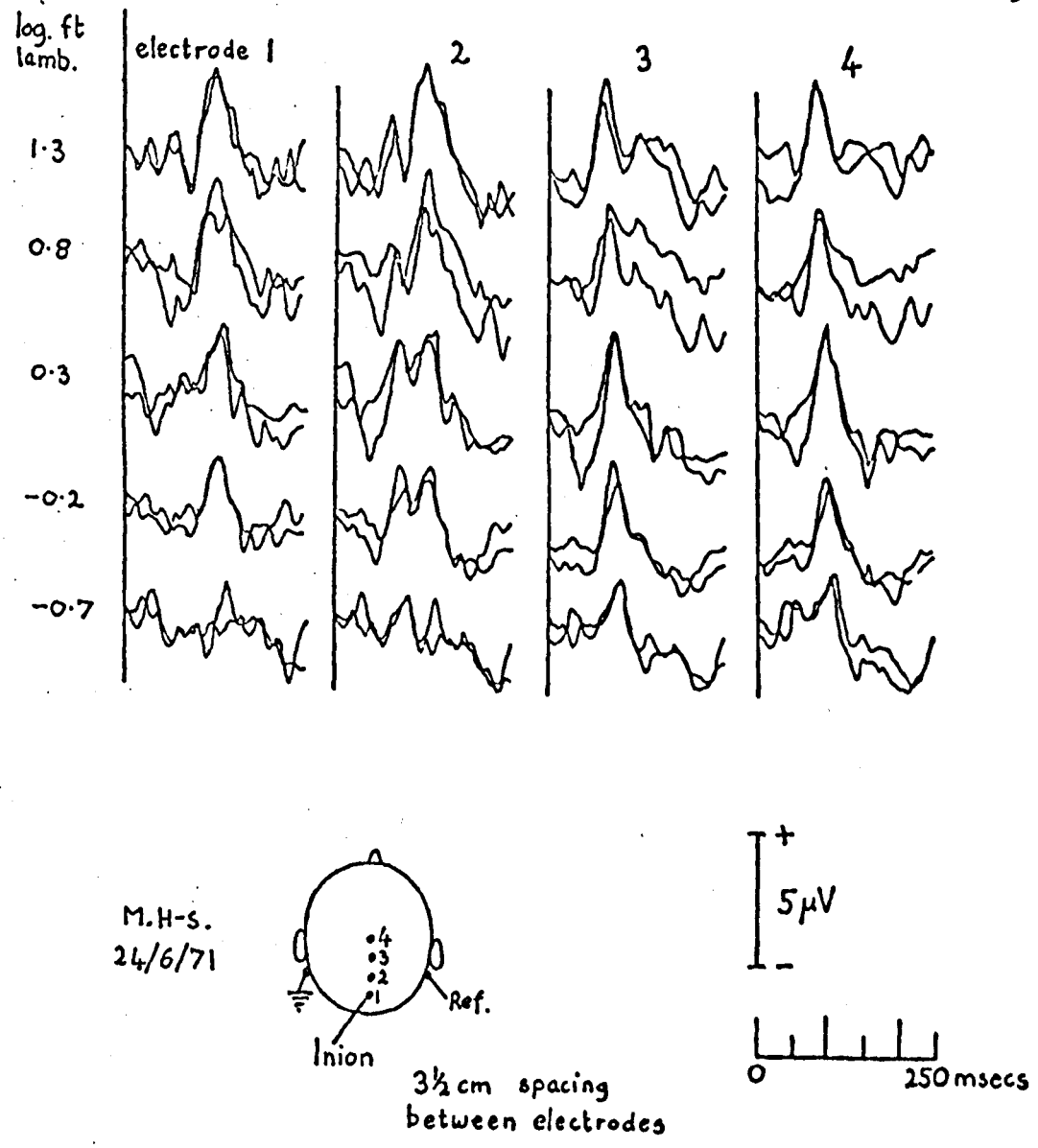

Fig.4.2.2. The effect on the motion-reversal VEP of varying the pattern brightness. (Velocity = 10°/sec). The large amount of noise makes interpretation more difficult, but the main finding that changes in brightness do not greatly affect the VEP except at the lowest brightness levels is unambiguously shown.

brightness levels even well into the photopic range (e.g. Fig. 4.2.2, electrode 2), but such differences were never very great. This experiment was performed on three subjects, with similar results for each.

4.2.2. The sharpness of the boundary of the visual field.

In view of the discovery by MacKay & Rietveld (1968) that the proximity of a stationary reference line enhances the VEP to onset of motion of a stimulus line, it might be expected that the sharp contours comprising the edge of the visual field would influence the VEPs to onset, reversal and offset of motion of the noise pattern (see section 1.2.4). As a control experiment, a photographically blurred surround to the visual field was used. This change did not affect the VEPs (Fig. 4.2.3), so it is concluded that the field surround did not exert any major reference contour influence on the VEPs. This experiment was performed on four subjects, with similar results in each case.

The above finding need not contradict MacKay & Rietveld's (1968) report that a reference line enhances the VEP to motion-onset, because the experimental conditions are different. In particular, they found that the reference line effect was limited to within 1° of the reference line, and such a localised effect might well not have been noticeable under the conditions of the present series of experiments; for only a small proportion of the stimulated visual field was within 1° (horizontally) from a near-vertical surround-edge and only vertical contours would be expected to exert a reference-line effect as the motion was horizontal.

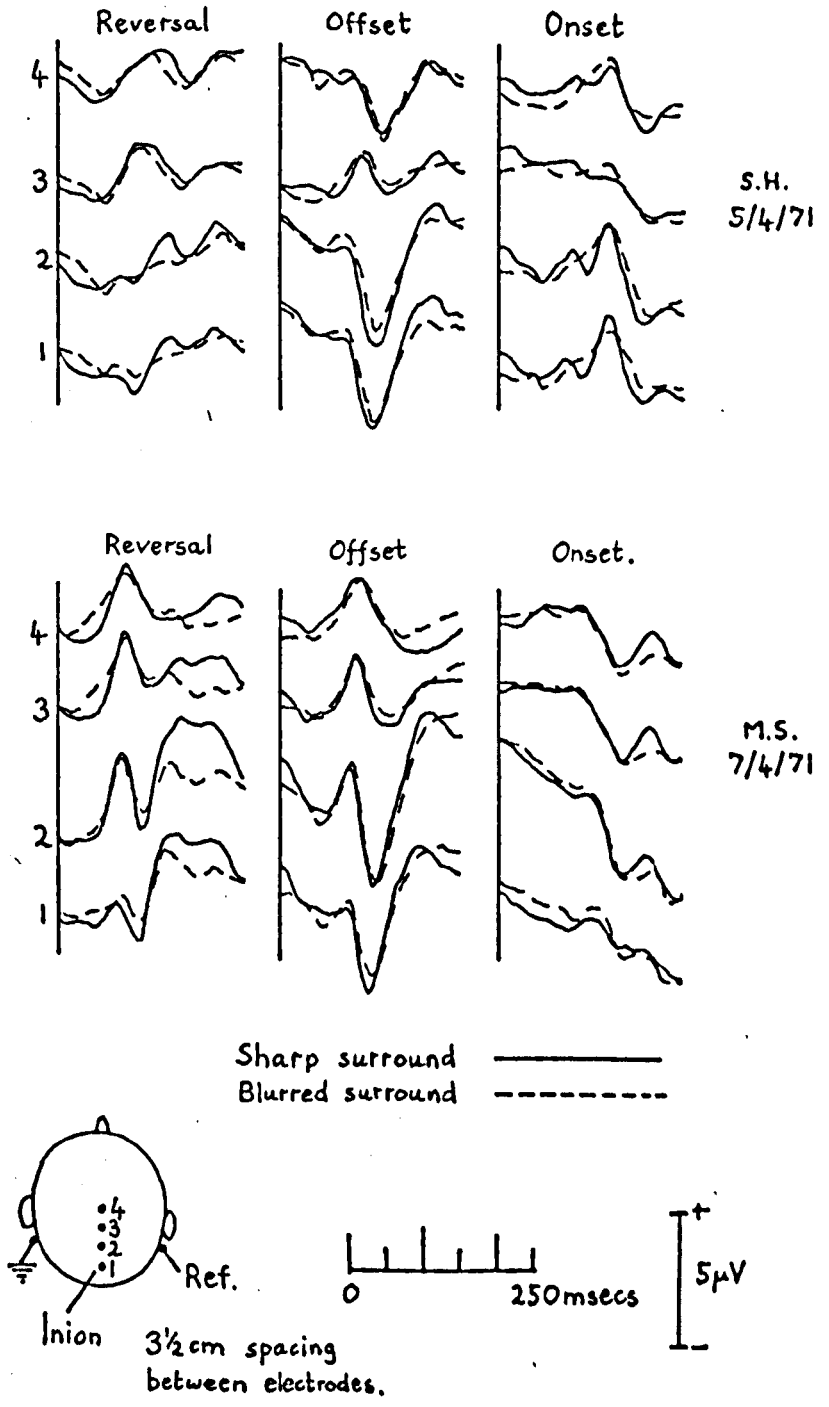

Fig.4.2.3. The effect of replacing the sharp field surround normally used with a blurred surround (4 radius, lower half-field in each case). There is no significant change in the VERs.

4.2.3. Superimposed steady velocity.

The effect of superimposing a steady velocity on the reversing waveform is illustrated (Fig. 4.2.4) for one subject. As one would expect, the 5°/sec motion-reversal VEP was gradually transformed into a 10°/sec onset or offset VEP, as the steady velocity in one of the two horizontal directions increased. Large superimposed velocities greatly reduced the VEPs and modified the waveform. These effects were investigated in four subjects, with similar results from each.

Rietveld & MacKay (personal communication) investigated the effects of larger velocities (± 5, ± 10, ± 15 °/sec) superimposed on a reversing 10°/sec motion. Both the forms and the magnitudes of the VEPs were strongly dependent on the superimposed velocity. Hence they concluded that the VEPs "do not reflect the stepwise velocity change as such". My results certainly corroborate this conclusion.

4.2.4. Direction of motion.

The VEPs to onset, reversal and offset of motion were not totally independent of the direction of motion, but the directional differences were quite small (Fig. 4.2.5). The differences were mainly in the amplitudes of the components, the basic waveform remaining the same for all the directions investigated. This experiment was carried out in two subjects, with similar results in each case.

Diagonal directions were not investigated in the present investigation. But Rietveld & MacKay (1968) compared VEPs to the reversal of motion of a line raster for eight different directions of stimulus motion, and found no significant dependence of the VEP on the direction. In this

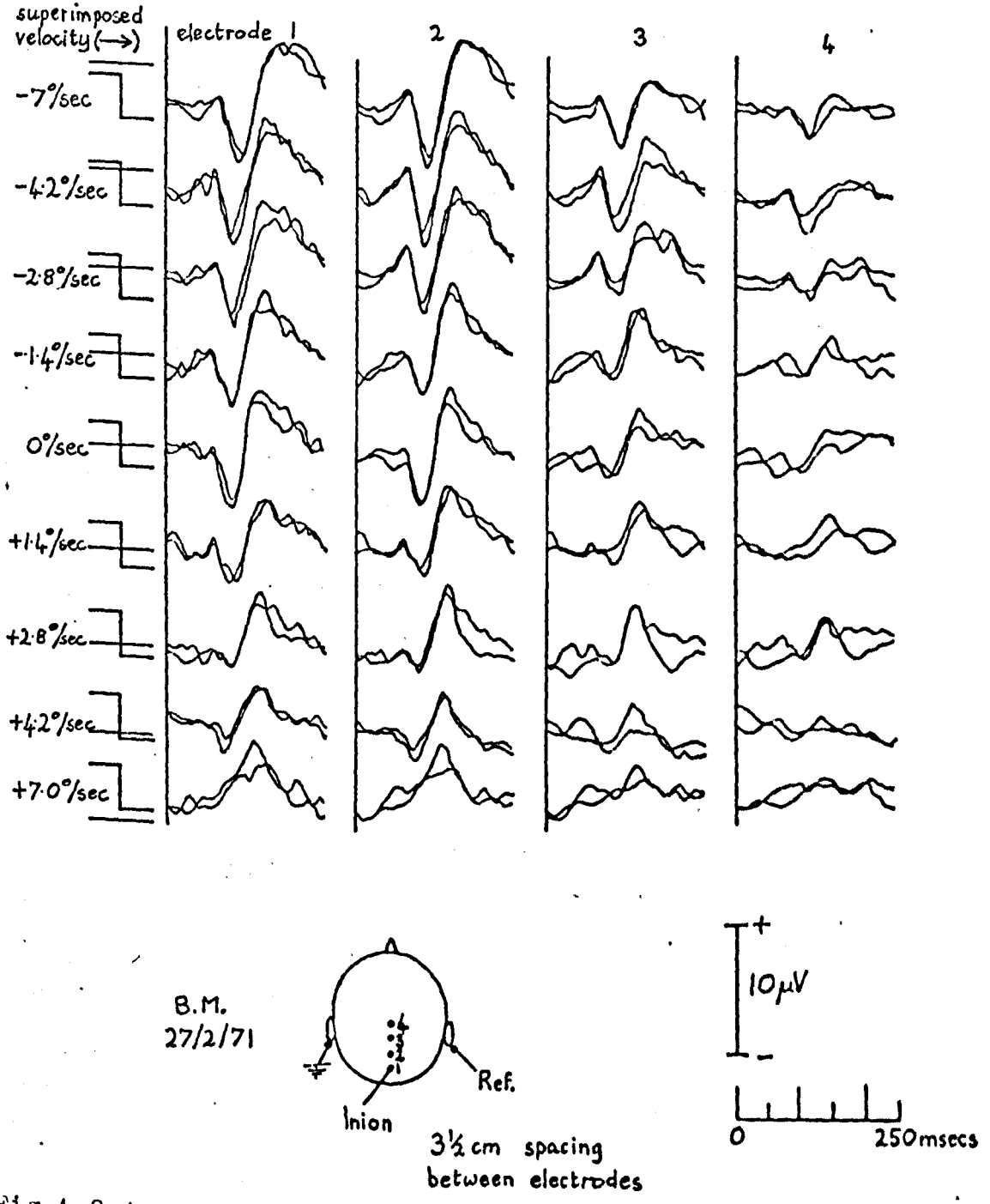

Fig.4.2.4. The effect of a steady superimposed velocity on the VEP to motion-reversal (5°/sec, → to ←).

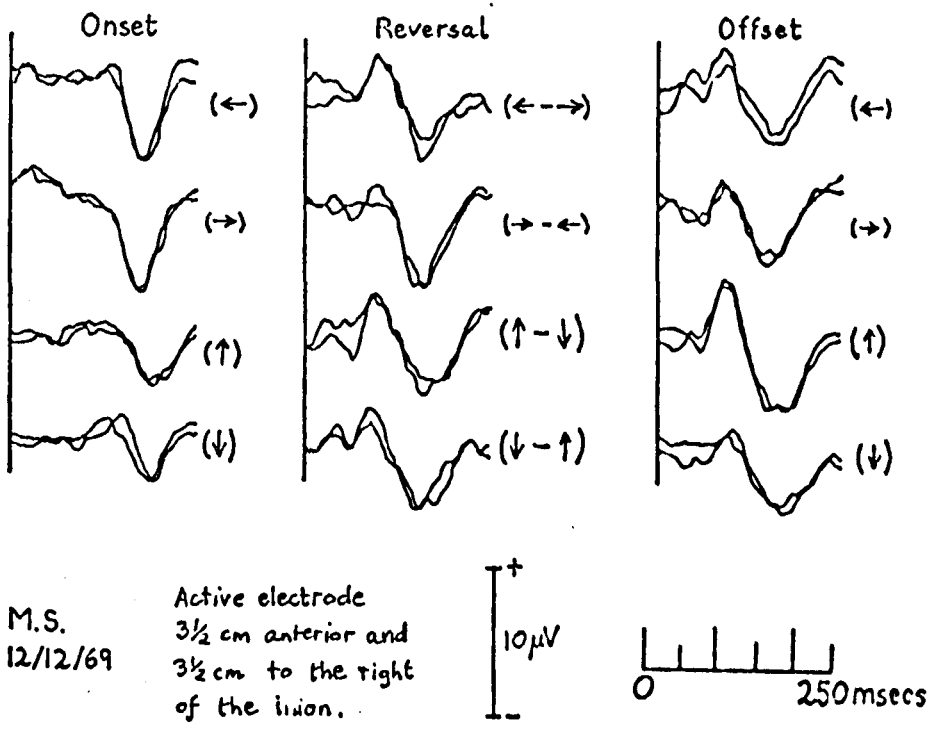

Fig.4.2.5. The effect of varying the direction of motion. Slight changes occur in all three kinds of VEP (i.e. onset, reversal, offset). These changes are changes in the amplitudes of the different VEP components; the basic waveform remains the same.

Velocity = 10°/sec. Visual field: 2.5 radius, whole field. (Whole-field stimulation was used because lower half-field stimulation would involve a horizontal edge through the centre of vision which might affect the VEPs to vertical and horizontal motion differently.)

respect motion-reversal VEPs seem to differ from the VEPs to grating-alternation reported by Maffei & Campbell (1970), as the latter VEPs were greater for vertical or horizontal bars than for oblique bars.

4.2.5. Pattern.

Noise was used as the stimulus pattern in most experiments, for the reasons stated at the start of chapter 3. In a few experiments, however, other patterns were used as well.

In fact, a checkerboard pattern (18' checksize) tended to produce motion-onset, offset and reversal VEPs fairly similar in form and amplitude to those produced by visual noise; but line rasters (21' period) produced VEPs different in form, and smaller in amplitude for motion-reversal and offset, but apparently slightly larger for motion-onset (Figs. 4.2.6 - 4.2.7). It would have been sensible to study the effects of incorporating breaks in the line rasters, but this was regrettably not done.

The effects of varying check size (Fig. 4.2.8) were investigated in four subjects. The optimal size of check varied between subjects and increased with velocity, and it was different for different VEP components; but for velocities between 3 and 20°/sec the optimal check size was always between 10' and 40', in onset, offset and reversal VEPs. These values are similar to those obtained for flashed pattern stimulation, for which the optimum check size is typically 10' - 20' (Rietveld et al., 1967; Harter & White, 1970).

Rietveld & MacKay (1969a, b) reported a double negative peak

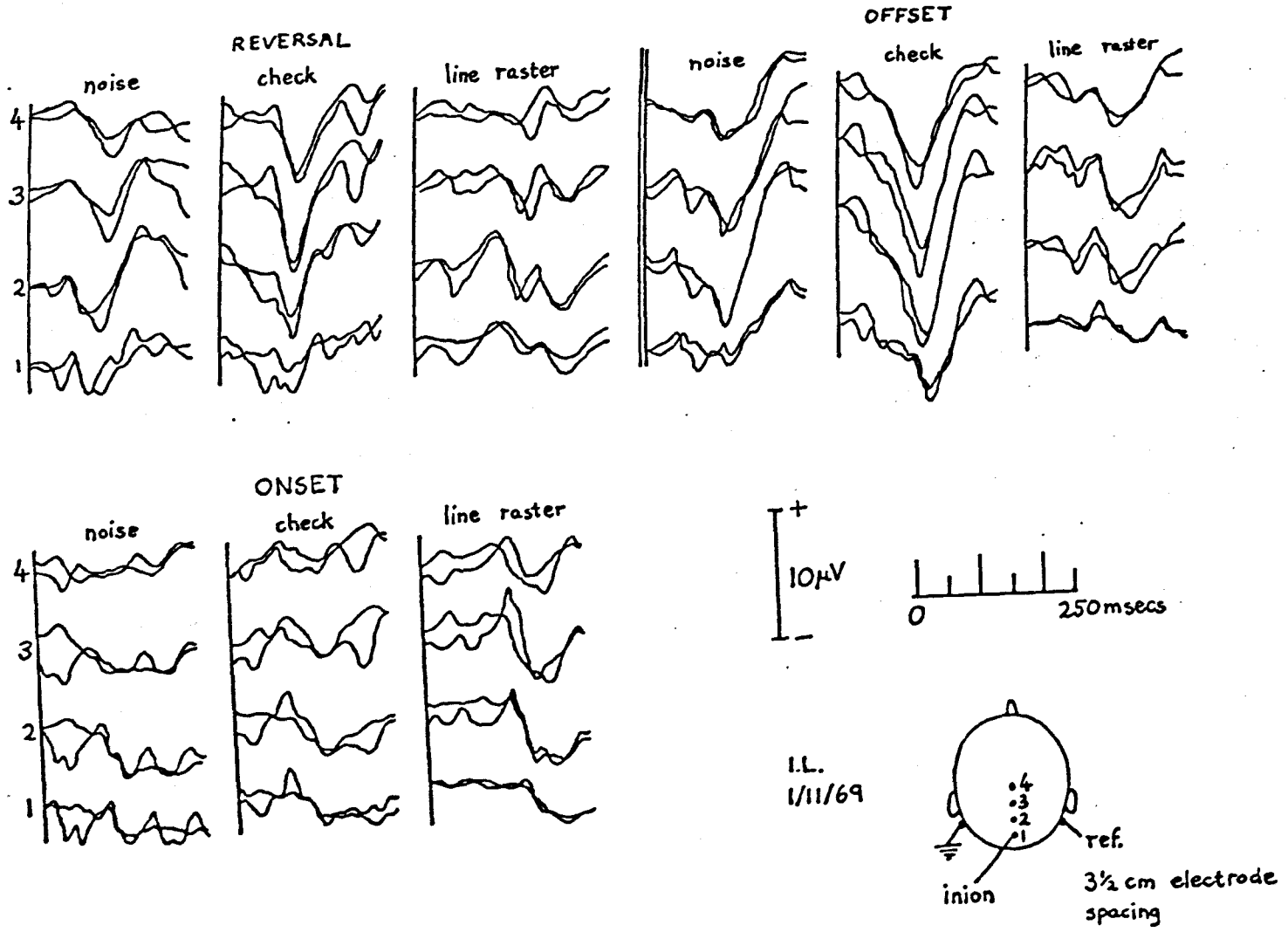

Fig. 4.2.6. VEPs to the onset, offset and reversal of motion of various patterns: visual noise, 18' checkerboard, 21' (period) line-raster. Velocity = 10°/sec. Field size = 2.5°

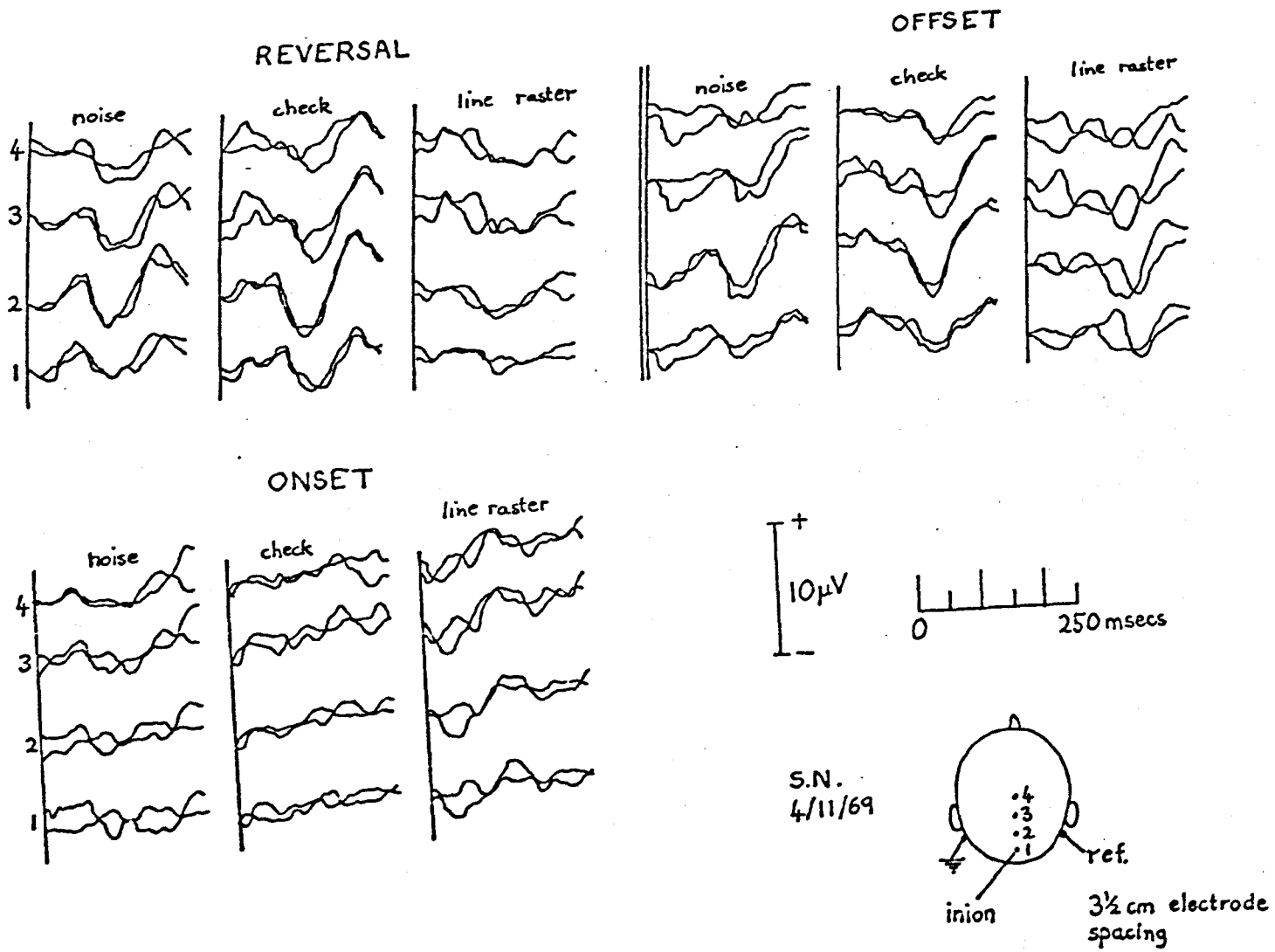

Fig.4.2.7. VEPs to the reversal, onset and offset of motion of various patterns: visual noise, 18' checkerboard, 21' (period) line-raster. Velocity = 10°/sec. Field size = 2.5°

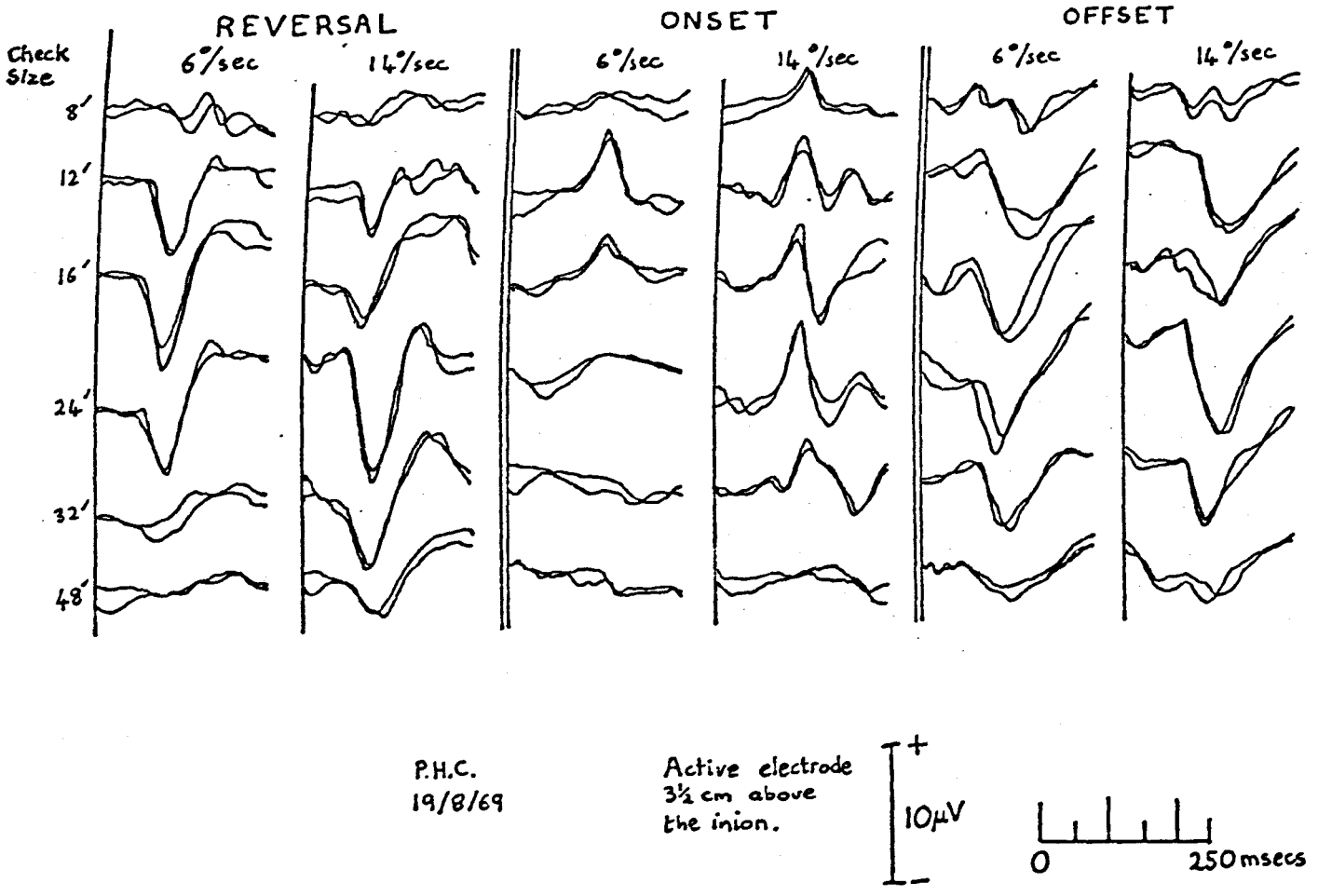

Fig. 4.2.8. The effects on the VEPs to reversal, onset and offset of motion of a checkerboard of varying the spatial frequency, illustrated for two velocities.

(93, 107 msecs in their figure, 1969b) for checkerboard motion-reversal (see Fig. 1.1.2), but such an effect was never observed in the present experiments (e.g. Figs. 4.2.6 - 4.2.8). Yet the combination of speed (12°/sec) and pattern size (19' checks) for which their double peak was most apparent was used in the present series of experiments for nine subjects. The discrepancy could be due to differences in experimental set-up. In particular, Rietveld & MacKay used 9° radius whole-field stimulation, whereas most of the checkerboard-motion experiments in the present series involved 2.5° radius lower half-fields. 5° radius whole-fields were used, however, for two subjects (including Fig. 4.2.8), but this is still substantially different from the field size used by Rietveld & MacKay. Also, the latter did not find their double-peak effect in all subjects (Rietveld & MacKay, unpublished data).

CHAPTER 5

Concluding discussion

5.1. Comparison between the present results and the related data of other investigators.

In the previous chapters, the present results have, to some extent, been compared with the related data of other investigators; but a few further comments are required.

The pattern-appearance VEPs reported in this thesis differed in no way from the published data of Jeffreys (1969, 1970b, 1971).

There were, however, marked discrepancies between my work and that of Rietveld & MacKay (1969a, b and unpublished data), probably because of the large differences in visual field in the two cases.

In addition to the discrepancies referred to previously (3.2.2, 4.2.6), the following must be mentioned.

(i) Rietveld & MacKay (unpublished data) found that the motion-onset and -offset VEPs were substantially smaller than the motion-reversal VEPs, and very different in waveform. This contrasts with my finding that the main components of the motion-offset VEPs were frequently larger than those of the motion-reversal VEPs, and the waveforms were similar in each case (although very different for motion-onset).

(ii) Rietveld & MacKay (unpublished data) found that the motion-reversal VEPs (peak-to-peak amplitude of largest components) increased monotonically in amplitude as the velocity increased from 1.5 to 15°/sec. (The stimulus pattern was visual noise.) I found that this was true for C1 (positive for lower half-field stimulation, latency 100 msecs), but that the later

components decreased as the velocity increased above about 8°/sec.

(iii) Rietveld & MacKay (1969b) reported that the latency of pattern-appearance VEPs, but not of motion-reversal VEPs, varied over the scalp. Using lower half-field stimulation, I found no variation of the latency of either kind of VEP over the scalp; but using whole-field stimulation, I observed latency variations for both kinds of VEP (cf. the findings of Jeffreys referred to in 5.2.2).

As already stated, all these discrepancies may be the results of differences in the visual field sizes used ($8\frac{1}{2}^{\circ}$ radius whole-field - Rietveld & MacKay; 3° lower half-field - Jeffreys; 4° lower half-field in my own experiments). Differences between the grain-sizes of the visual noise patterns used may have been an additional factor in causing the second discrepancy above (different effects of varying velocity).

Despite these discrepancies (which are only to be expected since the experimental conditions were different) there were a number of points on which my data agreed with that of Rietveld & MacKay (1969a, b).

(i) VEPs to motion-reversal and to pattern-appearance had very similar waveforms and distributions over the scalp (4.1.4).

(ii) The VEPs were largely independent of the brightness except at the lowest brightness levels (4.2.1). Even here there was some discrepancy, for Rietveld & MacKay (unpublished communication) found that this ceased to be true for brightness levels of 0.25 log. ft. lamberts or below, whereas I found it to be true down to -0.2 log. ft. lamberts. The cause of the discrepancy is unknown.

Marshall & Harden (1952) and Dawson et al. (1968) also found that

the VEPs to moving stimuli were not greatly affected by the brightness level.

(iii) The final conclusion of Rietveld & MacKay (1969a, b) that the mechanisms underlying pattern-appearance VEPs and motion-reversal VEPs are not identical suggests that direction-selective mechanisms contribute to the latter. My data support such a conclusion.

5.2. General discussion.

5.2.1. Are motion-reversal VEPs produced by direction-selective mechanisms?

The conclusion of chapter 3 is that the motion-reversal VEPs were probably produced largely through the activity of direction-selective mechanisms responding by virtue of their direction-selectivity. The evidence for this is divided into three sections.

(i) The fact that the motion-reversal VEPs were differently affected by adapting motions in opposite directions shows that direction-selective mechanisms contributed to the VEPs to some extent at least (3.0). It is difficult to avoid this conclusion, but the adaptation experiment certainly does not show the extent to which direction-selective mechanisms contributed.

(ii) Evidence has been presented that the 5 msec turn-round time was effectively instantaneous (3.1). This is what one would expect, as the maximum discrepancy between the actual waveform of reversal and the theoretical waveform of instantaneous reversal was very small: about 0.6' for 10°/sec motion, and proportionately more or less for larger or smaller velocities.

The strongest evidence that the finiteness of the 5 msec turn-round was not important lies in the fact that the VEPs were very sensitive to the steady velocity before and after motion-reversal, but insensitive to the

actual time course of reversal. It might be argued that increasing the turn-round time above 5 msecs did not affect the VEP because the effects due to the finiteness of the turn-round time had already reached saturation at 5 msecs. This argument is inherently unlikely, however, as the pattern-appearance VEPs required a much longer duration before saturating, as did the VEPs to a brief cessation of motion; and it does not explain the fact that the VEPs to reversal at 90°/sec were very small, even when the time-course of motion near the moment of reversal was made similar to that for 8°/sec motion. For example, one would expect direction-insensitive contrast-detectors to respond very much more strongly to the temporary stopping of a 90°/sec moving noise pattern (which appears very blurred) than to the stopping for a similar duration of a slower (10°/sec) moving noise pattern.

These conclusions are supported by the fact that a 5 msec cessation of motion produced very little VEP. And even the slight response which did occur to this stimulus may have been caused by motion-detectors responding to the change in velocity.

The fact that VEPs to brief (10 msec) presentations of stationary and of moving (8 or 10°/sec) patterns were similar is much weaker evidence. It suggests that the contrast-sensitive mechanisms underlying the VEPs required more than 10 msecs to discriminate between the stationary and the moving patterns, implying that these mechanisms would not be affected by a very brief (<5 msec) slowing down of a moving pattern. That is not necessarily valid, however, for there is no logical reason why a mechanism should not respond almost identically to two inputs, 'a' and 'b', but still be sensitive to a change from input 'a' to input 'b'. Even so, this line of

evidence does indicate that it is unlikely that contrast-sensitive mechanisms should respond significantly to the brief slowing down at reversal, which supports the stronger evidence mentioned previously.

The fact that tachistoscopic motion-reversal gave a reduced VEP is no evidence against the above conclusions, as a step-displacement 20 msec after the moment of mirror-produced reversal produced similar suppression without affecting the turn-round waveform. The significance of this effect is briefly discussed in section 3.1.5.

(iii) Finally, the possibility has been considered that direction-insensitive mechanisms might be activated even by instantaneous motion-reversal.

The fact that the motion-reversal VEPs were identical for periodic and aperiodic stimulation would seem to be a strong argument against eye movements being implicated in the production of the VEPs.

The investigation of possible VEPs due to contrast-enhancement during instantaneous reversal is less clearcut, as is the following section on statistical changes in the pattern of stimulation. The difficulty here is that not enough is known of the underlying processes to permit precise formulation of the ways in which contributions from direction-insensitive mechanisms might occur. All that can be said is that none of the admittedly simplistic tests which have been performed gives cause to suspect any significant contribution from direction-insensitive mechanisms.

5.2.2. What are the implications of the close similarity of the VEPs to motion-reversal, motion-offset and pattern-appearance, and of the VEPs to motion-onset and pattern-disappearance?

The above evidence suggests that the VEPs to motion-reversal reflect the activity of direction-selective mechanisms. Also, the fact that all but the first peak of motion-offset VEPs are abolished for very high stimulus velocities suggests that at least the later components of these VEPs are similarly the product of direction-selective mechanisms. Nevertheless, the close similarity of the VEPs to motion-reversal, motion-offset and pattern-appearance implies that closely related mechanisms are probably involved in all three cases. Likewise it would appear that closely related mechanisms underlie the VEPs to motion-onset and pattern-disappearance.

These similarities are, perhaps, surprising, and it must be admitted that the most natural interpretation would be that the VEPs to onset and offset of motion are caused largely by the resulting disappearance and appearance (respectively) of stationary pattern; and that the movement-reversal VEP is caused by a brief appearance of stationary pattern at the moment of reversal. But, as argued above, it is hard to explain on this view why only the first component of the motion-offset VEPs remains at high ($\sim$90°/sec) velocities, and nor why the motion-reversal VEP is greatly reduced at high velocities even when the turn-round time is increased using a low pass filter.

Nevertheless, it does seem likely that, in some way, mechanisms sensitive to stationary patterns (and perhaps inhibited by moving ones) are at least partly responsible for the motion-onset and -offset VEPs (motion-onset corresponding to pattern-disappearance, motion-offset to pattern-appearance).

Perhaps the simplest explanation of the similarity between motion-

reversal and pattern-appearance VEPs would be that motion-reversal causes the onset of stimulation of pattern-detectors sensitive to one direction of motion and the simultaneous offset of stimulation of pattern-detectors sensitive to the opposite direction. The resulting combination of VEPs would, if the interaction were not too grossly non-linear, probably resemble pattern-appearance VEPs, but would also include a smaller pattern-disappearance component; the latter might correspond to the apparent contribution of motion-onset mechanisms to the motion-reversal VEP (4.1.4), as motion-onset VEPs resemble pattern-disappearance VEPs. But this is all highly speculative, and the situation is no doubt much more complicated in reality.

5.2.3. An alternative hypothesis.

One more possible source of motion-reversal VEPs must be considered, however. Many neurones in striate cortex of awake monkey respond with a maintained discharge to a stationary stimulus, but some of these respond much less strongly to a moving stimulus (Wurtz, 1969a). It is likely that the latter effect is produced by inhibition from movement-sensitive mechanisms.

Now, in man, perception of the movement of a noise pattern moving to and fro is virtually lost if the frequency of alternation is above about 25Hz, which suggests that the movement-detecting system integrates with a time-constant of the order of 20 msecs. (20 msecs corresponds to a cut-off frequency of 8Hz.) It is possible that the hypothesized movement-sensitive mechanisms inhibiting stationary-stimulus-detecting units in monkey would exhibit a similar time constant of integration. If so, the movement-induced inhibition would integrate to zero very soon after the moment of reversal of motion of a stimulus pattern, permitting a response from the stationary-

stimulus-detectors; and similar mechanisms could be responsible for pattern-appearance VEPs in man.

This hypothesis is not contradicted by any of the experiments reported in this thesis. Even the modification of the motion-reversal VEP by a unidirectional adapting stimulus is compatible with it. The reduction of VEP at high velocity would be expected, as there would then, presumably, be no inhibition to be released during motion-reversal.

The hypothesis would explain the suppression of the motion-reversal VEP due to a step-displacement within about 20 msecs of the moment of reversal, as the step could produce an added burst of activity in the movement-detectors which would inhibit the stationary-pattern-detectors. The fact that greater suppression is produced by a step-displacement after the moment of reversal than by one before is correctly predicted.

Again, the very close similarity between the motion-reversal VEP and the VEP to a 20 msec stopping of the stimulus during continuing motion (Fig. 3.1.17) would also be explicable.

The hypothesis could be extended to account for VEPs to motion-onset and -offset. Assuming that the latter originate in the hypothesized stationary-stimulus-detectors, the hypothesis would account for the fact that the VEPs to motion-reversal, motion-offset and pattern-appearance are similar; and that those to motion-onset and pattern-disappearance are similar.

It is correctly predicted that VEPs to the appearance of moving patterns are smaller than those to the appearance of stationary ones, and that the difference is large for appearance-durations above about 20 msecs. For low velocities, the reduction is much less for C1 than for C2 and C3,

and this could explain why the optimal velocity for production of C2 and C3 in motion-reversal and -offset VEPs is lower than for the production of C1.

It should be noted that although the VEPs to the onset, reversal and offset of motion are, according to this hypothesis, generated in mechanisms responsive to stationary contours, the production of the VEPs is nevertheless dependent on the activity of motion-sensitive mechanisms. Whether the latter are direction-selective is not relevant to the hypothesis.

It is, of course, highly speculative, and probably oversimplified; but it does seem to account for all the experimental data.

5.3. Suggestions for further research.

A substantial weight of evidence has been presented indicating that the finiteness of the motion-reversal turn-round time is not responsible for any major components of the motion-reversal VEP. But the possibility that instantaneous motion-reversal might activate direction-insensitive VEP mechanisms has been less extensively investigated and cannot be ruled out. Indeed, one hypothesis as to how this might occur has been outlined above (sub-section 5.2.3). The extent to which motion-reversal VEPs reflect the activity of direction-selective mechanisms is therefore not yet conclusively established; for motion-onset and -offset VEPs the matter is still less certain. Therefore more work on these questions is required.

The hypothesis outlined in sub-section 5.2.3 is testable. It implies that the reduction of pattern-appearance VEPs if the pattern is moving, rather than stationary, is partly due to the activity of inhibitory mechanisms, and not merely to subjective blurring caused by the motion. This

could be investigated by studying pattern-appearance VEPs for stationary and moving patterns, varying the velocity, the focus, and the appearance-duration.

The interesting psychophysical experiments on saturation by Sekular, Pantle and others (see sub-section 1.2.1) suggest useful correlative VEP experiments. It was found that the contrast thresholds for moving bars were appreciably raised by the previous viewing of similarly oriented bars moving in the same direction, but not to the same extent if the bars were stationary or moving in the opposite direction (Pantle & Sekular, 1969). It would be interesting to investigate whether correlative effects were caused by the pre-exposure of stationary and moving patterns on VEPs to the sudden appearance of a moving pattern. (I did carry out a preliminary experiment on this, using noise patterns. The results indeed showed a reduction in VEP due to a pre-exposed pattern moving in the same direction as the stimulus pattern, but no reduction for one moving in the reverse direction or stationary.)

Pantle & Sekular (1969) interpreted their results as indicating the existence of two different classes of element, one (DS) sensitive to the direction of motion, the other (OS) sensitive only to the orientation of the stimulus bars. The fact that the hypothesized DS elements appeared to be much less sensitive to contrast than the OS elements suggests another possible correlation between VEPs and psychophysics; but it should be added that Rietveld & MacKay (1969a, b) did compare VEPs to motion-reversal and pattern-appearance, and found that both were very sensitive to reductions in contrast (see section 1.1.5).

The present thesis has been restricted to motion in one dimension.

The next stage would be to study transitions from motion in one dimension to motion in another. I did in fact study this very superficially, using the mirror system combined with a rotating disc in the projection plane to produce a transition from top-left-to-bottom-right motion to top-right-to-bottom-left motion. This produced a VEP similar to a motion-reversal VEP; but tachistoscopic switching from one direction of motion to a perpendicular one tended to produce a larger VEP than did tachistoscopic motion-reversal.

It would also be interesting to study VEPs to moving stimuli in the periphery of the visual field, for the extreme periphery of vision (in man) is especially sensitive to movement and the after-effect of seen motion is described by subjects as "more violent" in the periphery (Wohlgemuth, 1911). The results presented in this thesis are sufficiently firm and detailed to constitute normative data for central vision against which the data for peripheral vision could be compared.

Appendix 1. Determination of the time constant of the low pass filter required to transform the time-course of reversal of 90°/sec motion to be approximately the same as that of 8°/sec motion with no filter.

Denote time = t, velocity = V(t).

The time-course of reversal will be approximately the same, within a few msecs of the moment of zero velocity, in all cases for which the rate of change of velocity at the moment of zero velocity $\left(\frac{dV}{dt}_{(V=o)}\right)$ is the same. We first determine the relationship between V(t), the steady velocity Vo, and the filter time constant T.

Consider a perfect system for generating motion-reversal: before reversal, V = -Vo, changing instantaneously to +Vo at the moment of reversal.

If a step function from 0 to 2a at time t = o is passed through a low pass filter (time constant T), the output is $2a(1 - e^{-t/T})$.

Hence, if the input is from -a to 'a, the output is $2a(1 - e^{-t/T}) - a$

$$= a(1 - e^{-t/T})$$

Similarly, when the low pass filter is placed in the motion-control system, the velocity step from -Vo to +Vo becomes:

$$V(t) = Vo(1 - 2e^{-t/T}) \qquad (i)$$

$$\text{so} \quad \frac{dV(t)}{dt} = \frac{+2Vo}{T} e^{-t/T}$$

But when V(t) = o, $e^{-t/T} = \frac{1}{2}$ (from (i))

and hence, $\frac{dV}{dt}_{(t = o)} = \frac{Vo}{T}$

Now the system with no filter added behaved approximately like a perfect system with a filter of 1.6 msec time constant added, but this may

be neglected when a substantially larger filter is added as well.

Hence the filter time constant required to produce the same $\frac{dV}{dt}(t = o)$ for 90°/sec velocity, as for 8°/sec velocity without the filter is (from equation (II)):

$$= 1.6 \text{ msecs} \times \frac{90°/\text{sec}}{8°/\text{sec}} = \underline{\underline{18 \text{ msecs}}}$$

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