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CHANGES IN PATTERN-EVOKED RESPONSES IN MAN ASSOCIATED WITH THE VERTICAL AND HORIZONTAL MERIDIANS OF THE VISUAL FIELD

BY A. M. HALLIDAY* AND W. F. MICHAEL*
From the National Hospital for Nervous Diseases, Queen Square, London, W.C. 1

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SUMMARY

1. Averaged responses have been recorded from an array of ten scalp electrodes over the occipital cortex in man to the reversal of a black-and-white checkerboard pattern, presented in different octants of the visual field.

2. In all subjects a prominent wave was seen, with a peak latency of about 100 msec, which showed consistent and systematic changes with variation in the position of the stimulus in the visual field.

3. With stimulation of the octants next to the vertical meridian, this component was of large amplitude, while with stimulation of the octants next to the horizontal meridian, it was small and inconspicuous.

4. With upper field octants, the peak at 100 msec was surface-negative, while with lower field octants it was reversed in polarity.

5. The occipital response was largest 5 or 7·5 cm above the inion, and the amplitude recorded 3 cm lateral to the mid line was larger over the hemisphere contralateral to the half field being stimulated than ipsilaterally.

6. These findings are discussed in relation to the underlying anatomy of the visual cortex, and it is concluded that these responses are likely to arise mainly from extra-striate areas.

INTRODUCTION

Work on the cortical representation of the visual field in the cat (Bilge, Seneviratne & Whitteridge, 1963; Bilge, Bingle, Seneviratne & Whitteridge, 1967; Hubel & Wiesel, 1967) and the monkey (Talbot & Marshall, 1941; Daniel & Whitteridge, 1961; Myers, 1962; Cowey, 1964; Cragg, 1969;

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* Members of the External Staff, Medical Research Council.

Zeki, 1969) has shown that for each quadrant the vertical and horizontal meridians project to opposite edges of the corresponding area of V I in the striate cortex and that this arrangement is repeated twice in mirror image fashion in the non-striate areas V II and V III. In man, the clinical studies of Gordon Holmes (1918) and Teuber, Battersby & Bender (1960), and the investigations of Brindley & Lewin (1968) with a stimulating prosthesis laid on the calcarine region of a blind patient, have indicated that there is a similar arrangement of the quadrantic representation at least for the striate area. The foveal and para-foveal projections are at or near the occipital pole, and the more peripheral areas are represented progressively more anteriorly within the sagittal fissure. However, experimental studies in man have been limited, as opportunities for direct recording from the occipital cortex have been rare.

Relatively few records of evoked potentials from the scalp have been concerned with discrete stimuli in different parts of the visual field. Vaughan, Katzman & Taylor (1963) showed that responses to flashes covering the whole field may be diminished over the affected hemisphere in patients with visual field defects, and that this depression was largely dependent on macular field defects. Other workers, using small flashing spots of light subtending 1–2·5° have confirmed that foveal responses are larger than those to peripheral stimuli in healthy subjects (Copenhaver & Beinhocker, 1963; Copenhaver & Perry, 1964; Eason, Oden & White, 1967). Copenhaver & Perry (1964) found that the decrease in evoked potential amplitude was much the same whether the stimulus was moved peripherally along the vertical or horizontal meridian. Eason, White & Oden (1967) have shown that there is an increase in peak latency as the stimulus is presented more peripherally, and that the amplitude is significantly smaller when the stimulus is presented in the upper field rather than in the lower field.

Differences between the responses evoked by pattern stimuli presented in the upper and lower visual field have been reported by Jeffreys (1969) who noted a reversal in the polarity of certain components. He suggested that this polarity reversal was most readily explained if the responses were being generated in the regions of striate cortex inside the calcarine fissure, where the cortical layers representing the upper quadrants would be inverted in relation to the overlying cortex representing the lower quadrants (Jeffreys, 1969, page 214). If this explanation is correct, the reversal should be seen particularly well with stimulation of those areas of the upper and lower visual fields adjoining the horizontal meridian, because it is this part of the field which is represented within the calcarine sulcus. On the other hand, little or no polarity reversal would be expected on stimulation of the areas of the upper and lower fields adjoining the vertical meridian, which are represented on the medial surface of the cortex within the sagittal fissure, where the neurones lie parallel with each other.

The present experiments were undertaken to see whether there were important differences in the responses to stimulation of the visual areas alongside the vertical and horizontal meridians. A reversing checkerboard pattern of constant mean luminance was used, and in order to cover a sufficient visual area to produce good responses, this occupied a 45° segment of the central 7–9° of the visual field, placed with its apex at the subject's fixation point. A preliminary communication on these results is appearing elsewhere (Michael & Halliday, 1970).

METHODS

Eleven subjects were used, aged between 19 and 46 years, all right-handed. Ten chlorided silver cup electrodes were fixed to the scalp with collodion over the occiput, together with a distant reference electrode, variously 10 cm above the nasion (called 'mid-frontal'), 5 cm below the inion (called 'mid-cervical'), and the two ear lobes linked. The array of occipital electrodes, whose general configuration is shown in Fig. 2, were spaced 3 cm apart laterally and 2·5 cm apart antero-posteriorly. The most posterior line of electrodes was situated either at the level of the inion or, more usually, 2·5 cm anterior to it. Monopolar recordings of each of the ten occipital electrodes were made in every run, using one of the three references.

The subject was comfortably seated 1 m from a translucent screen on which the stimulus was back-projected. A wedge-shaped reversing checkerboard pattern was generated by alternately projecting a slide and its negative from two projectors fitted with electronically controlled shutters. The transition time of the shutters (open-to-closed or closed-to-open) was 8 msec. The stimulus wedge subtended an angle of 7–9° from the fixation point, which was provided by a small constantly illuminated spot of light at the apex of the wedge. The brightness of the white squares as seen by the subject was 108·5 cd/m^2, and the black squares 6·8 cd/m^2, and the individual squares subtended an angle of 50′. The stimulus was presented in a different octant of the visual field for each run (Fig. 1).

The operation of the shutters triggered a small digital computer averager (Halliday & Pitman, 1965) twice a second. Each pair of complementary reversals of the pattern thus occupied one second, and a hundred such pairs were given in each run. Responses were generally averaged over the 250 msec immediately following a pattern reversal, although in a few cases a longer period was used. Four channels were averaged at the time of the experiment; the other six channels were recorded on FM tape and averaged subsequently.

Recording was carried out in a darkened room. Subjects were instructed that during the actual runs they must be still, relaxed, and should concentrate on the stimulus while constantly fixating the spot provided. Any run in which the subject was aware of having allowed his gaze to wander, or in which excessive muscle potentials were apparent on the oscilloscope, was discarded and repeated. In spite of the shortness of each run, experiments tended to be lengthy. Two hours was usually as much as subjects could tolerate before becoming tense and lacking in concentration. For this reason, although some subjects were recorded during more than one session, in only one subject were recordings made of the responses to the stimulus in all eight octants of the visual field with each of the three reference electrodes. For the same reason in only a few cases was a second run given for particular octants to demonstrate the repeatability of the responses.

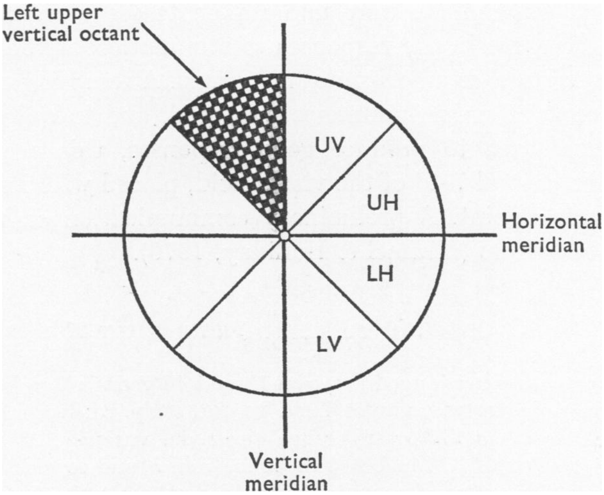

Fig. 1. The octants of the visual field and their nomenclature as used in this paper. In each half field these were: upper vertical (UV), upper horizontal (UH), lower horizontal (LH) and lower vertical (LV). The stimulus, an alternating checkerboard pattern, was presented in any one of the eight octants, and is shown in the left upper vertical octant. The central fixation point is also shown.

RESULTS

In this paper the octants of the visual field in which the stimulus was presented will be called 'upper' and 'lower' according to their relation to the horizontal meridian, and 'vertical' or 'horizontal' according to which meridian they adjoin. In each half field the stimulus could therefore be presented in one of four octants, upper vertical, upper horizontal, lower vertical or lower horizontal (Fig. 1).

In spite of considerable inter-subject variability in wave form, all the subjects showed a prominent wave in their average response to pattern reversal with a peak latency between 80 and 120 msec. This wave varied consistently and systematically in size and polarity according to the particular octant of the visual field being stimulated. In most subjects this was the largest and best defined wave recorded during the 250 msec averaging period and had a consistent peak latency of 100 msec. In a few experiments, the responses were averaged over the whole half cycle (500 msec), but as this failed to show any other features of interest, and decreased the resolution of detail in the earlier components, only the 250 msec immediately following the stimulus was averaged in most experiments. The direction of pattern reversal was found not to be a significant variable, as responses to alternate half cycles, averaged separately, had the same waveform as responses to the pairs of complementary pattern reversals averaged together.

The results reported here will concentrate on the characteristics of the wave occurring at 100 msec, and measurements of its amplitude will be arbitrarily defined as the vertical distance from the peak (or trough) of this wave to the peak of the following wave of opposite polarity. An upward deflexion of the record in Figs. 2, 4 and 5 indicates a negativity of the recording electrode with respect to the reference; for this reason measurements made from the peak of an up-going wave at 100 msec are given as minus figures, measurements from a down-going wave at 100 msec as positive figures.

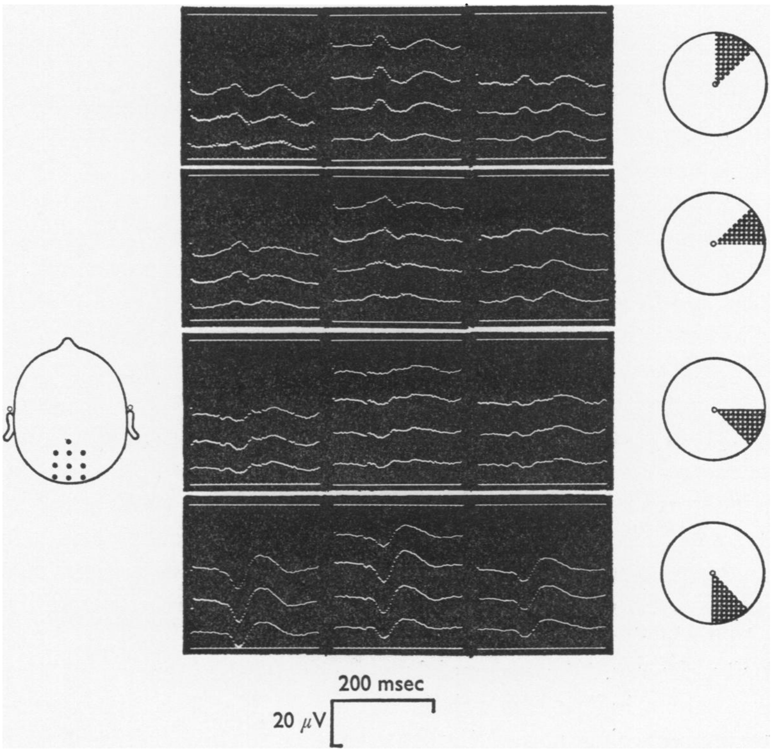

Fig. 2. Averaged responses to an alternating checkerboard stimulus presented in four different octants of the right half field (indicated to the right of each set). The layout of each of the four sets of records corresponds to the arrangement of electrodes used, shown in the head diagram. These are monopolar recordings (negativity upwards) with the two ear lobes joined as reference. Subject N.L., aged 22 yr.

Fig. 2 illustrates responses that are typical of those found in the whole series and demonstrates a number of general features which will be considered in more detail. Stimuli in the vertical octants produced large well defined responses whereas those in the horizontal octants produced responses of small amplitude, which were sometimes ill defined. Upper field octants produced a negativity of the component at 100 msec, while with lower field octants this component had a positive polarity. Responses to stimuli in one half of the visual field were larger over the contralateral than the ipsilateral hemisphere, and with both upper and lower field stimuli, the responses of maximum amplitude were recorded fairly high up on the head above the inion, generally at the 5 or 7·5 cm electrode.

Vertical/horizontal octant differences. Vertical octants were very effective stimuli. Generally the lower vertical octant produced slightly larger responses than the corresponding upper vertical octants, as in Fig. 2, but in some subjects there was little difference, and in a few the upper vertical octants produced slightly larger responses than the lower vertical. Fig. 3 plots the amplitude of maximum responses recorded in the mid line at 100 msec for each of the eight octants in six subjects in whom a two-ear reference was used. The individual values are plotted as solid circles, and the means are joined by the continuous line. Amplitude measurements obtained from recordings with the mid-frontal and mid-cervical reference electrodes are also plotted in Fig. 3, as open circles and open squares respectively, to show their general correspondence with the two-ear values. As not all octants have been recorded in each subject and there is some overlap in subjects, the latter values have not been used in calculating means. The difference in size between responses to stimuli in the vertical and horizontal octants is clearly seen.

Polarity changes. The reversal in polarity of the component at about 100 msec shown in Fig. 2 is well illustrated in Fig. 3, the negative upper field responses lying above the base line and the positive lower field responses below it. This reversal with upper and lower field stimulation was seen in all subjects without exception with the vertical octants. With the horizontal octants the same rule of polarity generally held true, although in some cases the components were less easily definable. Fig. 4, which shows recordings from the same subject as Fig. 2, demonstrates that the polarity reversal occurs independently of the reference electrode chosen. This establishes that the change in polarity was truly a function of the occipital generator and is not an artefact produced by the reference electrode. Polarity effects dependent on the reference electrode should be reversed by changing from a mid-frontal reference, well above the generator level, to a mid-cervical reference, well below the generator level; in practice the polarities for each octant remained unchanged, whether a mid-frontal, two-ear or mid-cervical reference was used. However, the responses were not entirely unaltered by a change of reference electrode, and some modification in the amplitude and gradient was seen.

A few subjects were 'anomalous' in that the upper horizontal octant response resembled the corresponding lower octant in having a positive instead of a negative peak. In some cases the horizontal octant response took a transitional form. An example is shown in Fig. 5. This subject showed large and clear up-going peaks at 95 msec with the left upper vertical octant stimulus, and down-going peaks at the same latency with the left lower horizontal and left lower vertical octant stimuli. With the

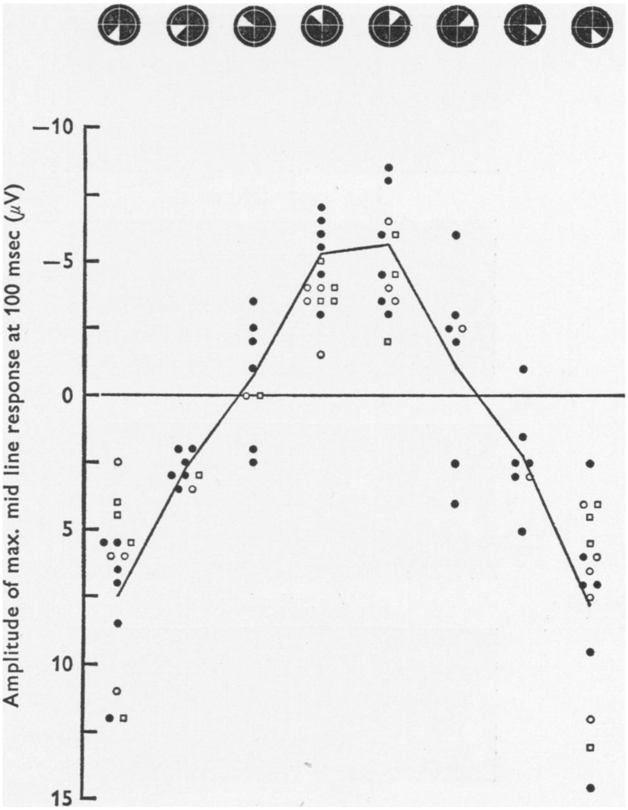

Fig. 3. Amplitude of the largest response recorded from the mid-line electrodes for stimulation of each of the eight octants of the visual field (indicated above). Values for responses in six individual subjects in recordings with a two-ear reference are plotted individually (●), and the mean amplitudes for all six are joined by the continuous line. For comparison, values for individual responses using a mid-frontal (○) and mid-cervical (□) reference are also shown.

left upper horizontal octant stimulus, however, there is a down-going peak, but this is now superimposed on a longer-lasting up-going wave, as is shown by the negative peaks at 70 and 105 msec.

Laterality differences. Responses to octants in one half of the visual field produced responses larger over the contralateral hemisphere than the ipsilateral. Fig. 6 shows the relative size of responses over the left hemisphere, the mid line and the right hemisphere for the same six subjects as Fig. 3, each column representing the mean amplitude of the responses at the electrodes 2·5 and 5 cm above the inion. It will be seen that the mid-line response was usually intermediate in size between that from the electrodes 3 cm to the right or left of the mid line, but was sometimes larger even than the contralateral response. The differences between the ampli-

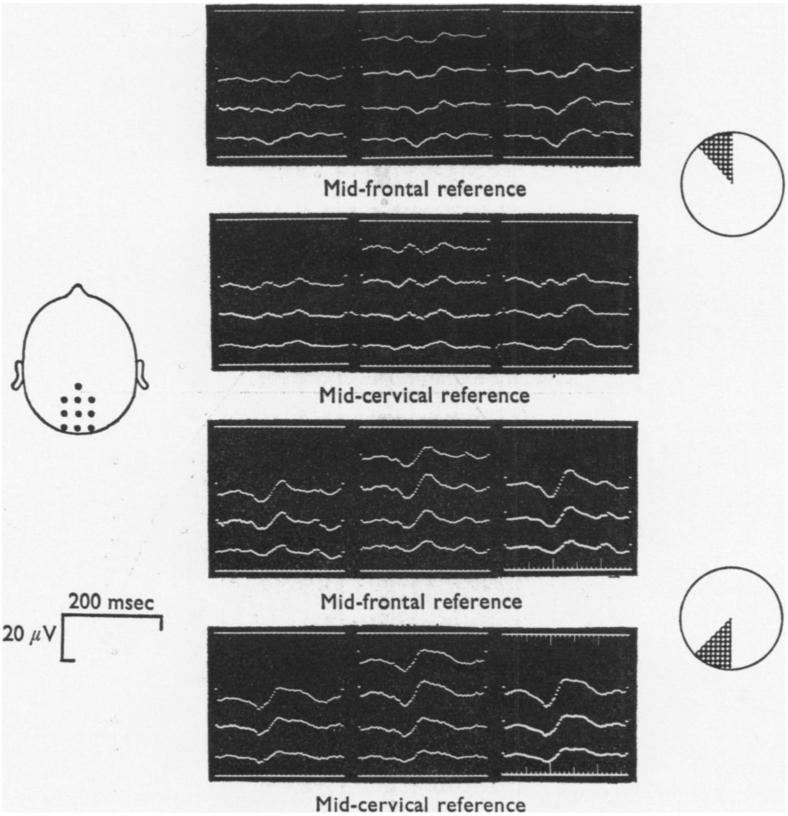

Fig. 4. Responses from the same subject as Fig. 2, to show the effect of changing the reference electrode. The upper two sets of records show responses to stimulation of the left upper vertical octant, and the lower two sets to stimulation of left lower vertical octant.

tude of the response recorded from the ipsilateral and contralateral electrodes were highly significant for most octants (Fig. 6).

Position of maximum amplitude in the antero-posterior axis. Fig. 7 shows the mean amplitude of the response, together with the standard error, for the different mid-line electrodes for the same six subjects as in Figs. 3 and 6. The electrodes 2·5, 5 and 7·5 cm above the inion were used for all six subjects, but the electrode at the inion itself was used only in the first two subjects. With the other four subjects, it was felt more useful to include the electrode 10 cm above the inion. Unfortunately, the equipment in use did not allow more than ten channels to be recorded simultaneously. The means for the inion electrode are therefore derived from only two subjects, and those for the electrode 10 cm above the inion only from four subjects; this partly explains the somewhat higher standard errors for the means in these positions.

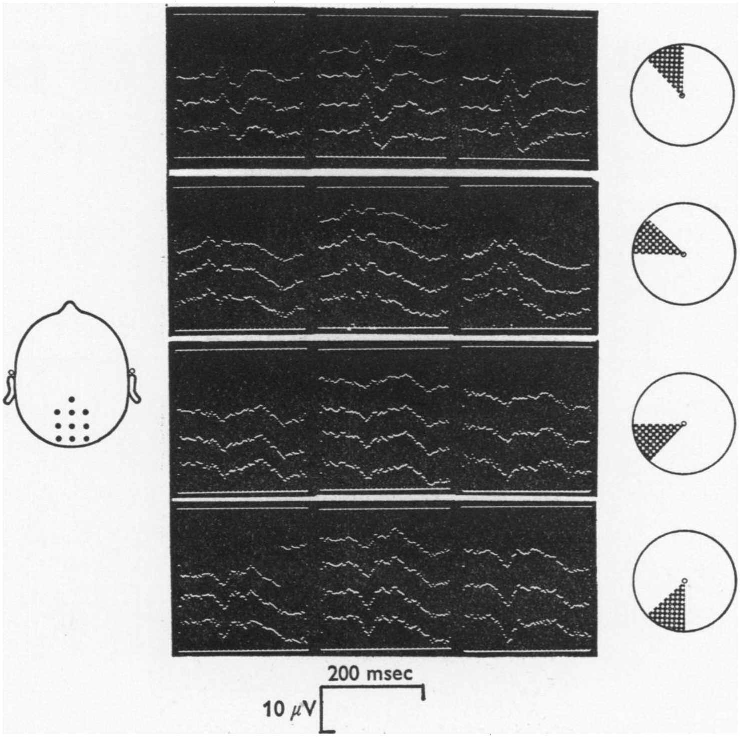

Fig. 5. Averaged responses of another subject (N.E. aged 36 yr) to stimulation of the octants of the left half field. Otherwise as in Fig. 2. Note 'transitional' triphasic wave form to stimulation of upper horizontal octant.

It can be seen from Fig. 7 that the maximum voltage for both upper and lower vertical octants is located some way above the inion, at the 5 or 7·5 cm electrodes. There is also a suggestion in Fig. 7 that the maximum is slightly more posterior for the lower vertical octants than for the upper vertical octants, but this trend does not reach statistical significance.

Octant responses to patterned flash. As most previous evoked potential studies have used flashed stimuli, it was felt worth while comparing these responses with those to a similar patterned stimulus flashed in each octant

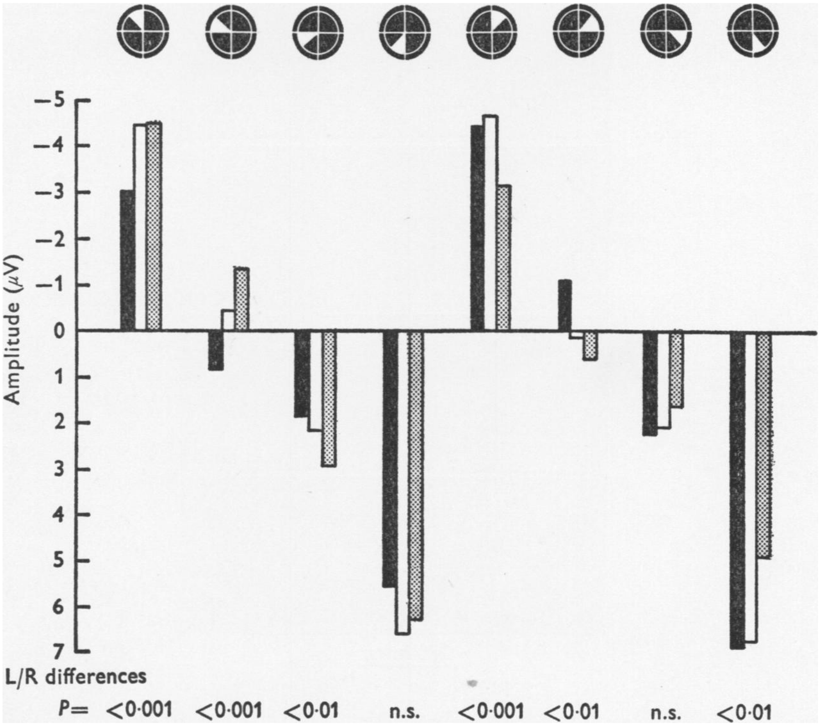

Fig. 6. The mean amplitude of responses recorded at the 2·5 and 5 cm electrodes in the same six subjects as Fig. 3. Values from left-sided (stippled) mid line (white) and right-sided (striped) pairs of electrodes are plotted separately for each octant to show laterality differences. The significance of the left/right differences is indicated below (two-tailed *t* test).

of the visual field. One of the two slides of the checkerboard wedge stimulus was projected onto the translucent screen as before, but the bulb of the slide projector was replaced with an electronic flash lamp, flashed twice per second. Thus the stimuli occupied the same position and visual angle as before, but the alternation of pattern with constant over-all illumination was replaced by a repetitive flash stimulus. This arrangement produced rather featureless sinusoidal occipital potentials without any characteristic clearly repeatable from subject to subject. In one or two runs a small inflexion could be discerned at about 100 msec superimposed on a larger rising or falling wave, reminiscent in shape and polarity of the dominant wave seen at that latency when the alternating checkerboard stimulus was used on the same subject, but in most cases there was no detectable component at 100 msec and no reversal of polarity of any other wave.

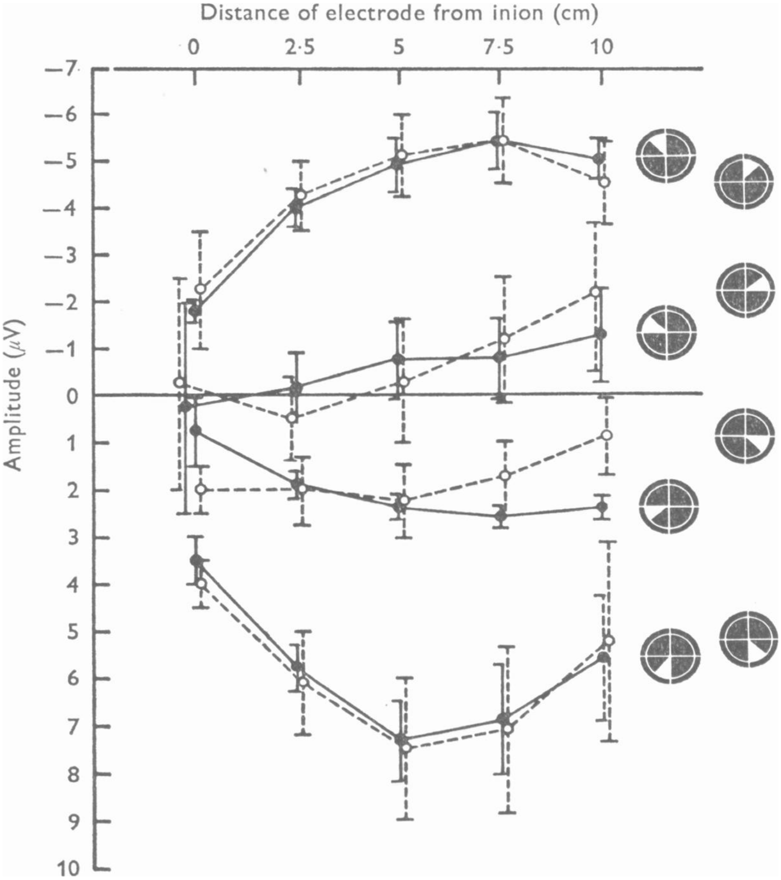

Fig. 7. The mean voltage gradients in the antero-posterior axis for the same six subjects as in Fig. 3 and 6. The mean amplitude ± S.E. is plotted for each of the mid-line electrodes. The S.E.S are somewhat higher for the inion and 10 cm electrodes as these were not recorded in all subjects (see text).

The topographical distribution of the maximum amplitude of these flash-evoked responses closely followed that already described for the constant illumination experiments, in that amplitude tended to be greatest 7·5 cm above the inion, and laterality differences were similar. However, flash octant responses differed in one interesting respect; upper octants tended to be much less effective than lower, and in some subjects responses showed a progressive increase in size, with upper vertical octants the smallest, then upper horizontal, lower horizontal and finally lower vertical octants the largest. This was seen in subjects who showed the quite different pattern described above in the experiments with checkerboard alternation under conditions of constant over-all illumination.

DISCUSSION

These results clearly confirm the polarity reversal reported by Jeffreys (1969) in his experiments with alternate checkerboard/blank field stimulation of the upper and lower quadrants and half fields. However, the striking polarity reversals in the present experiment were seen with stimulation of the vertical, rather than the horizontal, octants, and this appears to rule out his suggestion that the responses originate in the neurones *inside* the calcarine sulcus, where the neurones for upper and lower fields are inverted in relation to each other. The work of Gordon Holmes (1918) and Brindley & Lewin (1968) has made it clear that the vertical octants of the visual field are represented in the cortex outside the calcarine fissure in man, as in the monkey, and that the striate cortex within the calcarine fissure is concerned with the horizontal octants.

The fact that stimulation of the horizontal octants produced such small responses in the present experiments might suggest that, if the responses were arising mainly from the striate cortex, those from within the calcarine fissure were being greatly attenuated by their site relative to the recording electrode. If this were so, the large amplitude response showing polarity reversal might be being recorded, not from the mass of cells within the calcarine sulcus, but from those neurones on the lips of the sulcus adjoining the sagittal fissure whose fields could be detected by the recording electrode on the scalp. It might then be supposed that the large reversed responses were produced by the vertical rather than the horizontal octant stimuli because the area represented by these neurones on the calcarine lip fell just within the vertical octants. It is, of course, difficult to explain the polarity reversal as originating in the cortex representing the rest of the vertical octants, because this lies on the medial surface of the occipital lobe, and the neurones representing the upper and lower fields are lying parallel to each other in a horizontal orientation. The data of Holmes (1918) and Brindley & Lewin (1968) suggest that the neurones lying on the lip of the calcarine sulcus would correspond to a line very near to the junction of the vertical and horizontal octants used in the present experiment. This hypothesis was therefore tested in three subjects by comparing the responses to a stimulus of the same size straddling the vertical and horizontal meridians, thus well away from the area represented on the calcarine lips. Contrary to prediction, the responses to octant stimuli straddling the upper and lower vertical meridians were large and showed the typical reversal of polarity, while the horizontal responses were of low voltage. Again contrary to prediction, stimuli centred over the 45° junction of the vertical and horizontal octants were not more effective than stimuli in the vertical octants.

Jeffreys' explanation implies that the cortical generators concerned lie in the striate area, but there is evidence which makes this unlikely. The striate representation of the central para-foveal visual field lies posteriorly at the occipital pole, with more peripheral areas represented progressively more anteriorly on the medial surface of the hemisphere and in the calcarine sulcus. The data of Holmes suggest that the central 9° of vision, from which responses were evoked in the present experiment, is represented in the posterior part of the striate cortex lying roughly between the surface markings of the inion and the 2·5 cm electrodes. However, the maximum amplitude of responses in the present experiments was recorded a further 2·5–5 cm in front of this for both upper and lower vertical octants, suggesting an extra-striate origin. The largest amplitude responses, to both the alternating and the flashed checkerboard, were usually recorded at the electrode 5 or 7·5 cm in front of the inion. In this respect pattern-evoked responses appear to behave similarly to responses to unpatterned flash stimuli. Doty (1958) first pointed out that the largest flash responses in cats were to be found with extra-striate recordings, and this was confirmed by Bilge *et al.* (1963) who found maximal responses towards the anterior part of V II.

If the responses are in fact arising from non-striate areas, another explanation must be found for the polarity reversal. One possibility to be considered is that the lower field generator lies on the upper convexity of the hemisphere while the upper field generator is on the under surface of the lobe. In this case, however, the lower field neurones would lie very close to the recording electrodes, while the upper field neurones would be remote. The rather similar amplitudes for upper and lower octant responses make this unlikely. It is true that lower vertical octant responses were on the average somewhat larger than upper vertical responses, but the difference was not great and in some subjects this relationship was actually reversed.

Another possible explanation of the polarity reversal is that it arises, not from two sets of generators lying as geometrically opposed dipoles, but from two distinct sets of neuronal elements situated in the same general area of cortex, whose activation produces surface potentials of opposite polarity. Depolarization occurring at different depths in the cortex may produce surface potentials of opposite polarity (Bishop & Clare, 1952; Carter, Holmes & Houchin, 1969). The well marked horizontal stratification of the striate cortex has been shown to have correlations with some functional differences; for instance, there is the segregation of simple cells in layer IV and of complex and hypercomplex cells in layers I to II and V to VI in area 17 of the monkey (Hubel & Wiesel, 1967).

At some stage in the analysis of the visual input, convergence of information from upper and lower quadrants must occur in order to allow comparison of features of stimuli lying across the horizontal meridian in one half field. There is already some electrophysiological evidence for cross-connexion between quadrants. Brindley & Lewin (1968) have found in man that stimulation of a point on V I which, near threshold, produces a phosphene at a point in the visual field corresponding to classical topography, sometimes produces on stronger stimulation a phosphene in a roughly corresponding point of the other quadrant of the same half field. If the evoked responses in the present experiment are being produced, at least in part, in an area of convergence of information from the two quadrants, the polarity reversal might be explained by a different distribution of afferent connexions for the two quadrants to different layers of the cortex.

We should like to thank Mr J. R. Pitman for invaluable technical assistance.

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