

Source Locations of Pattern-Specific Components of Human Visual Evoked Potentials. I. Component of Striate Cortical Origin

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Summary. A study was made of the transverse distributions of human scalp-recorded potentials evoked by the brief presentation of a pattern into different regions of a continuously illuminated diffuse field. The first two components of these visual evoked potentials (VEPs), designated C.I. (latency 65—80 msec) and C. II (latency 90—110 msec), were both greatly influenced by the retinal location of the stimulus pattern. In an initial study of the VEP waveforms with 12 subjects, followed by a more detailed investigation of the distribution of the individual components in 4 subjects, the following results were found.

1. Corresponding peaks (C. I and C. II) of the VEPs to stimulation of the upper and lower half-fields were inverted in polarity.

2. For the left and right half-field VEPs, the transverse distribution of C. I, but not of C. II, showed a polarity reversal across the midline.

3. Consistent differences were observed between the distributions of C. I for adjacent upper and lower quadrants, as well as between those for adjacent horizontal and vertical octants of the upper field.

4. Subjects differed in the degree of left-right asymmetry shown. There was also a much greater degree of interindividual consistency of quadrant and upper and lower half-field VEPs than for full-field or left and right half-field responses.

5. For C. I, an additive relationship was demonstrated between the half-field and the constituent quadrant VEP distributions.

These results indicate that C. I and C. II have spatially separate sources. Assuming a simple dipolar model based on the known retinotopic organization of the striate cortex, it is shown that the measured distributions are compatible with the hypothesis that component C. I, but not C. II, originates in striate cortex, from surface negative cortical activity.

Key words: Visual evoked potentials — Cortical sources — Man

Introduction

In contrast to the mass of reported data describing various parametric characteristics of (averaged) visual evoked potentials (VEPs) recorded from the human

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scalp, there is comparatively little information on the relationship between these surface responses and their underlying sources. Most components of the generally polyphasic VEPs are accepted as being of cortical origin, but as yet the exact source locations of individual VEP components within the various regions of the visual (and perhaps in some cases nonvisual) cortex remains undefined. This and the following paper describe how studies of surface VEP distributions can not only distinguish between VEP components having spatially separate sources, but also provide information on the actual source locations of these individual components.

A patterned (contoured) stimulus field was used in these experiments in preference to the more commonly used but physiologically less significant flash-illuminated diffuse field. The existence of pattern-related VEP components was originally reported by Spehlmann (1965) who compared the responses to flash presentation of patterned and diffuse fields. There is strong evidence (Jeffreys, 1968; Rémond *et al.*, 1969; White, 1969; MacKay and Jeffreys, 1972) to suggest that if a pattern stimulus involving little or no change in overall luminance is used, then the initial (pattern specific) components of the resulting VEPs are independent of the apparently more complex 'flash' VEPs. The relevance of such pattern stimuli for investigation of the physiological basis of VEPs is evident from the fact that the majority of single units in the visual cortex of cats and monkeys (Hubel and Wiesel, 1962, 1965, 1968), and probably of man (Marg *et al.*, 1968), are contour-specific and respond only weakly, if at all, to diffuse illumination.

By contrast with 'flash' VEPs, which appear rather insensitive to retinal locus (Rietveld *et al.*, 1965; Jeffreys, 1969; Michael and Halliday, 1970; MacKay and Jeffreys, 1972; but see also Biersdorf and Nakamura, 1971) these pattern-specific responses show very interesting changes with the retinal site of stimulation. There are marked differences in the VEPs obtained to stimulation of different regions of the visual field, a striking example being the polarity reversal of corresponding peaks of the midline VEPs to stimulation of the upper and lower halves of the visual field (Jeffreys, 1969; Halliday and Michael, 1970; MacKay and Jeffreys, 1972; Tweel, L. H. van der *et al.*, 1971). Also, Jeffreys (1969, 1971b) has shown that for the VEPs obtained to brief pattern presentations there is an additive relationship between the responses obtained to full-field stimulation and those of the constituent half- and quadrant fields.

Jeffreys (1969) has suggested that the observed variations of the VEPs with retinal location could most readily be explained in terms of the topography of the retinotopically organized visual cortex. On this basis, the polarity reversal of upper and lower field VEPs could be explained by the inverted orientation of the striate cortex forming the 'floor' and 'roof' of the calcarine fissures. However, following further studies (Jeffreys, 1970, 1971a, b) which showed that different components of these responses had different longitudinal distributions, it became evident that only the initial component distribution (typical latency 80 msec) was compatible with a source location in the striate cortex. The distributions of the second component (typical latency 110 msec) were better explained in terms of sources in extrastriate cortex on the under- and upper surfaces of the occipital lobes, associated with upper and lower regions of the visual field, respectively.

The work reported in this paper extends these investigations, and shows how studies of *transverse* distributions provide supporting evidence for the striate cortical origin of the first, but not of the second, component of these responses.

Methods

Stimulation

Pattern stimuli were presented by means of a tachistoscope consisting basically of two optically superimposed circular fields. Two stimulus conditions were used: (a) for the initial experiments with 12 subjects (data shown in Figs. 3 and 5), a field size of 3° radius, of typical luminance 1.0 log ft. Lamb. (34 cd./m^2) and viewing distance 1 m; and (b) for subsequent computer-controlled experiments with 4 subjects (data in all other figs.), a 6° field, luminance about 2.2 log ft. Lamb. (540 cd./m^2), viewed at 50 cm.

Each tachistoscope field consisted of an opal glass sheet transilluminated by three small fluorescent tubes (MAZDA MP 6w). The two sets of tubes were each connected in series with a variable resistor (intensity control) and a switching power transistor, controlled by one of the outputs of a bistable unit. The two fields were thus alternately illuminated. The tube switching times were about 300 μsec .

Stimulus patterns, drawn in black ink on tracing paper (or photographic transparencies) were placed in one field and unpatterned tracing paper in the other. The pattern used was a regular array of isolated squares, square side and separation being 14 min of arc. (This pattern was known to produce large amplitude VEPs). Similar small crosses, drawn on both clear and patterned tracing paper and optically aligned by the subject between runs, provided a steady central fixation mark. The stimulus was viewed binocularly.

The patterned field was illuminated for a duration of 25 msec and presented aperiodically with an interstimulus period which varied randomly between 585 and 735 msec for the computer-controlled experiments. The subject thus saw for most of the cycle a uniformly illuminated diffuse field, which was at aperiodic intervals replaced for 25 msec by a patterned field.

Procedure

The subject, seated comfortably in an undarkened soundproof room, was alerted by a warning 'buzz'. The responses for the first 5 or 6 stimulus presentations thereafter were not recorded. At the end of each run of about 35 seconds, the subject relaxed for a few minutes before the next 'buzz'. The subjects task during the run was merely to fixate on the central cross. The total length of a session was usually between one and two hours.

Recording

The EEG recording and VEP computation for the initial experiments were basically similar to those described previously (Jeffreys, 1971b), except that transverse electrode arrays were used.

For the computer-controlled experiments simultaneous monopolar EEG recording was made from 14 (or 16) electrodes, usually a longitudinal row of 8 midline electrodes, and a horizontal transverse row of 7 (or 9) electrodes, whose centre electrode was common to the longitudinal row. The level of the transverse row was determined from a pilot study of the midline longitudinal distribution. For 3 subjects, the common electrode was 5.0 cm above theinion, for the fourth subject (S.H.) it was 2.5 cm. Electrode separation was 2.5 cm except for the three most anterior electrodes where it was 5 cm. The most posterior midline electrode was 2.5 cm below theinion. The right earlobe was used as reference and the left earlobe grounded.

Only the results from the transverse electrodes are presented in this paper; those of the simultaneously recorded longitudinal responses are reported in the following paper (Jeffreys and Axford, 1972).

The amplified EEG signals were fed to the computer (PDP 8) A/D converters and sampled every 4.7 msec for a period of 300 msec after the start of the stimulus. Averaging was done 'on-line' and the accumulating responses displayed on a CRT. At the end of each run the computer performed the calculations described in the next section and then stored the results on magnetic tape.

Two averaging runs, each of 50 presentations, were carried out for each stimulus condition.

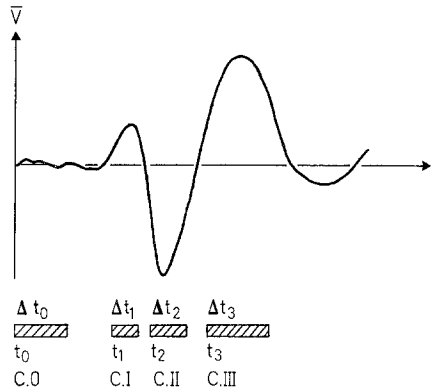


Fig. 1. *Method of computing response component amplitudes.* The mean value of the averaged EP during each of the preassigned sampling periods C.I, C.II, etc. is computed according to the formula given below. C.0 is a 'zero level' sample subtracted from all the others. Stimulus onset occurs at t_0 .

$$C.I = \frac{1}{\Delta t_1} \int_{t_1}^{t_1 + \Delta t_1} \bar{V}(t) dt - \frac{1}{\Delta t_0} \int_{t_0}^{t_0 + \Delta t_0} \bar{V}(t) dt$$

and similarly for C.II etc.

Computation of Component Distribution

After each run the averaged responses and their standard deviations were stored in the computer, which then entered a routine which computed the amplitudes of the various components. Sampling periods, at latencies selected to pick out the major components of the response (as determined in pilot experiments), were assigned prior to the experiment and the computer calculated the average value of the response during these periods (see Fig. 1). A 'zero level' sample (0—40 msec of the VEP) was also taken and all subsequent samples were measured with respect to this. Calibration pulses (10 μ V) were used at the beginning of the experiment to assign scaling factors automatically for each channel in the computer. This calibration was checked at the end of the experiment. Figs. 6—10 show plots of the mean value of the component amplitudes for the two repeated runs.

Repeatability of the various distributions obtained in this way proved to be very good, although sometimes identical stimulus conditions gave the same shape of distribution but with a shifted zero. This was often traced to different value of the 'zero level' sample, a difference which was common to all electrode positions. Thus the shape of the distribution was preserved even in the presence of zero-level shifts. This demonstrates the necessity for *simultaneous* recording from all electrodes when measuring distributions.

Errors

The PDP 8 also calculated the standard deviations (s.d.) of the averaged responses. These were displayed 'on-line' and provided a useful check on the correct functioning of the recording system. They were subsequently used to estimate the variability of the measured distributions. The s. d. values varied with electrode position, but were relatively independent of stimulus condition. Most electrodes showed a s. d. of about 1.2 μ V. The ± 1 s. d. deviation bars were computed for each experiment but are shown only in Fig. 6, and these should be taken as representative for the plots in Figs. 7—10.

Results

VEP Waveforms and Retinal Locus

There appear to be three major components in the first 150 msec or so of the VEPs obtained to the sudden brief presentation of pattern in place of a contin-

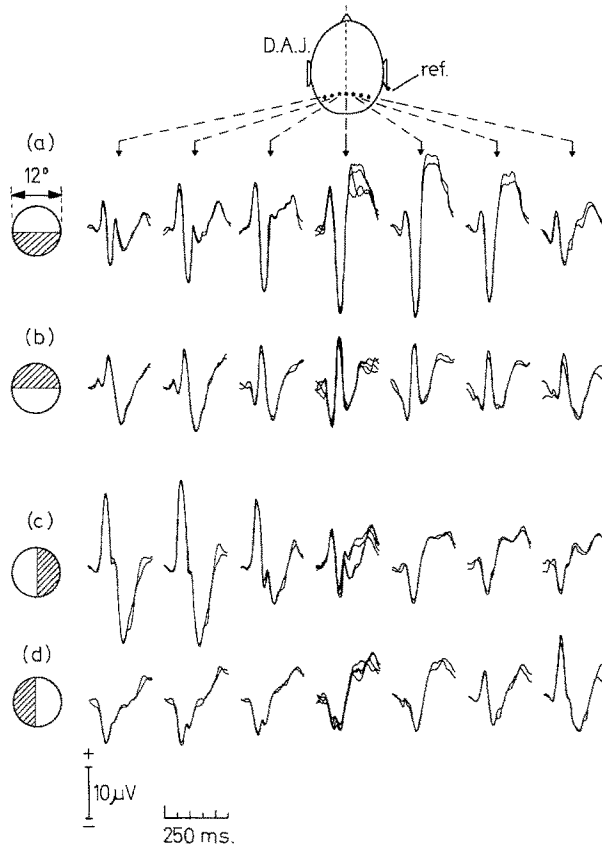


Fig. 2. *VEPs to half-field pattern stimulation.* Responses recorded from the transverse row of electrodes to stimulation of the (a) lower, (b) upper, (c) right, and (d) left half-fields. (In this case the VEPs from electrodes to the left and right of the midline were recorded in separate runs, the midline electrodes being common to both recordings.) The responses obtained for two identical stimulus conditions have been superposed in each case. The start of the trace coincides with the pattern onset. *Note:* In this and all other figures, the shaded area within the circle denotes the patterned region of the stimulus field. Also the left-right arrangement of the VEPs corresponds to that of the electrodes as shown on the diagram. This figure clearly illustrates the marked influence of retinal stimulus location on these VEPs. The basic form of the lower and upper field responses (a and b) does not change with electrode position although individual components appear to have different amplitude distributions. Corresponding peaks of the upper and lower field VEPs however are of opposite polarity. The left and right half-field VEPs (c and d) show considerable changes with electrode position, with the initial component changing polarity across the row of electrodes. There is a marked asymmetry in the left-right distribution of this component for the left and right field stimulation

uously illuminated diffuse field. These components vary in amplitude and polarity with retinal stimulus position and recording electrode, and in some experimental situations are difficult to distinguish, but they do not seem to vary significantly in latency for the retinal locations described in this paper.

Figure 2 shows typical half-field responses recorded from a transverse row of electrodes. Consider first the lower- and upper field VEPs (Fig. 2a and b). The

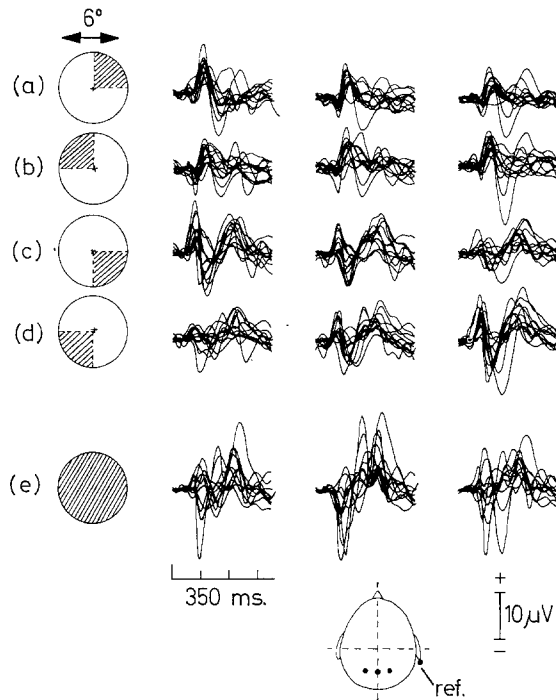


Fig. 3. *Interindividual comparison of VEP waveforms.* Superposition of the responses recorded from 3 transverse electrodes for 12 subjects to stimulation of each quadrant (a—d) and of the full (3° radius) field (e). Electrodes located on, and 3 cm to either side of, the midline, 3 cm above theinion. These results indicate a higher degree of interindividual consistency of VEP waveform for quadrant field than for full field stimulation. They also indicate a difference of distribution of the initial component of the upper and lower quadrant VEPs

basic triphasic form of these responses is seen at all electrodes, but the individual components have different amplitude distributions. The most striking difference between these results for the lower and upper half-fields is the polarity reversal (at corresponding latencies) of the components of these triphasic responses. The initial component (positive for lower field VEPs) starts some 40—50 msec after the stimulus and peaks at about 60—70 msec. This is followed by a component of opposite polarity, peaking prominently at about 90—100 msec. The experiments reported here deal only with these two components which appear to be related almost entirely to the “pattern appearance” (i. e. the transition from the diffuse to patterned field). We shall term the first component C. I and the second C. II.

Unlike those for the upper and lower half-fields, the VEPs to stimulation of the right and left half-fields (Fig. 2c and d) change considerably across the electrode row. There appears to be a polarity reversal of the initial component C. I, but not of C. II, although the behaviour of this and later components is not very clear from visual inspection alone.

A greater degree of interindividual consistency was found in the waveforms of upper and lower half-field and quadrant VEPs, than for full-field and left or right half-field responses recorded from the same electrodes. This is illustrated in

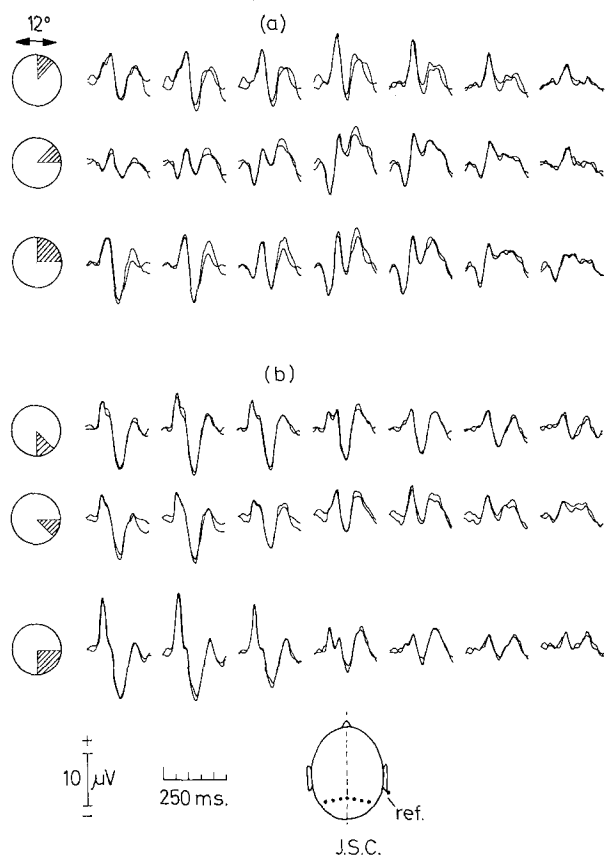


Fig. 4. *VEPs to quadrant and octant stimulation.* Responses recorded from the transverse row for subject J.S.C. to stimulation of (a) right upper and (b) right lower octants and quadrants of the visual field. These results indicate a difference in polarity and in distribution of the initial component of the 'vertical' and 'horizontal' octants of the upper quadrant which is not apparent for corresponding lower field octants. The initial component peak of the upper quadrant VEP is negative with a maximum slightly to the right of the midline, whereas the corresponding peak of the lower field quadrant has a maximum well to the left of the midline

Fig. 3 in which are superimposed the mean VEPs to stimulation of each quadrant and the full (3°) field, obtained from three electrodes (on, and 3 cm to either side of, the midline) for all twelve subjects of the initial study. This figure also indicates a difference in the transverse distribution, as well as in polarity, of C. I for the upper and lower quadrants (Jeffreys, 1970a). Whereas for the upper quadrants, C. I is negative, small and fairly symmetrical about the midline, for the lower quadrants C. I is clearly asymmetric, showing a relatively large positive amplitude at the contralateral electrode which drops abruptly across the midline.

Consistent differences were also observed between VEPs to stimulation of the two component octants of a given quadrant, especially in the upper field. Figure 4 shows the VEPs from a transverse electrode row to stimulation of the (a) upper and (b) lower right quadrants and octants of the field. For the upper

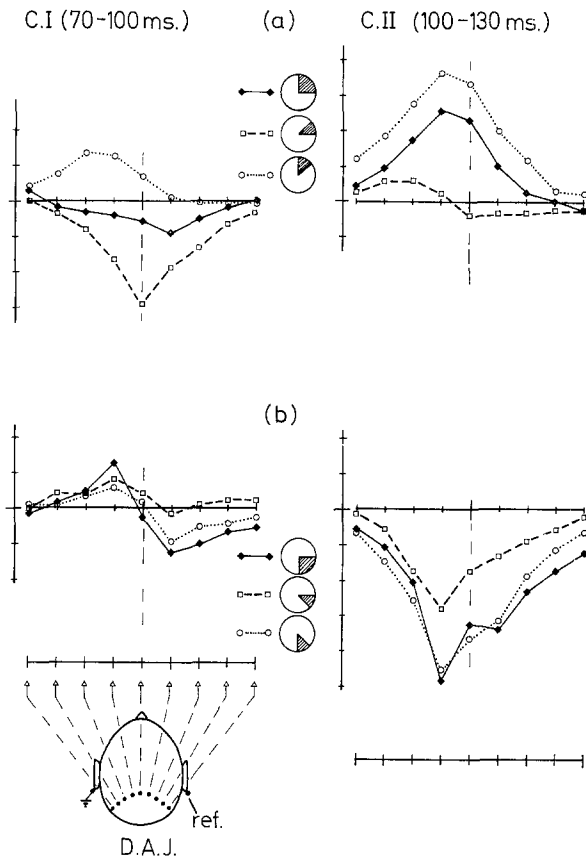


Fig. 5. *Transverse amplitude distributions of VEP components C.I and C.II.* Manually computed distributions of components C.I (70—100 msec) and C.II (100—130 msec) of the VEPs to stimulation of (a) upper, and (b) lower right quadrants (—) and horizontal (- - -) and vertical (. . . .) octants of the 3° radius field. This illustrates more clearly the different transverse distributions of the initial component of the upper vertical and horizontal octant VEPs indicated in Fig. 3 (for a different subject). The two octant distributions for the lower quadrant are more similar. There is also a marked difference in distribution of C.I for the two quadrant fields. The transverse distributions of C.II have different characteristics being largely monopolar with a contralateral maximum for both upper and lower field VEPs

quadrant VEPs C. I is negative with a maximum slightly to the right of the midline. For the upper horizontal octant C. I is also negative but with a more symmetrical distribution about the midline, whereas for the upper vertical octant it is positive at most electrodes. There are changes in form but not of polarity of C. I for the lower horizontal and vertical octants. For the lower quadrant, C. I is positive with a large amplitude at contralateral electrodes which drops rapidly across the midline.

Individual Component Distributions

More accurate measurements of the individual components of these responses showed features which were not obvious from the direct recordings. The inte-

grations required to measure these components were first done manually, but were later carried out by the computer as described in the Methods section.

Figure 5 demonstrates the different forms of amplitude distributions of C. I for the upper and lower field VEPs and the differences between the distributions of C. I and C. II for the same VEPs. Here the transverse distributions across 9 electrodes were calculated manually for C.I (70—100 msec), and C.II (100—130 msec) for right upper and lower quadrant and octant stimulation. (Note: The latencies of C.I and C.II are greater here than in Figs. 6—13 because of the lower luminance of the field in this case). The distribution of C.I for the upper quadrant is shallow and monopolar with a negative ipsilateral maximum, whereas that for the lower quadrant has a positive contralateral maximum and reverses polarity across the midline. These differences in distribution appear to result from the different C.I distributions for the constituent octants. For the upper field, the two octant distributions are markedly different; the vertical octant distribution has a positive contralateral maximum whereas that for the horizontal octant is wholly negative with a sharp maximum at the midline. For the lower field, the two octant distributions of C.I are more similar, each having a positive contralateral maximum.

The distributions of C.II do not show the same variations as those of C.I, for the different quadrants and sectors, being in almost all cases monopolar with a broad contralateral maximum (Fig. 5b). The upper horizontal octant distribution of C.II does show an apparent polarity reversal across the midline but this can be attributed to the overlapping of a basically positive component with the preceding large negative peak.

The degree of left-right symmetry of the transverse distributions of C.I for stimulation of corresponding regions in the left and right visual field was found to vary for the different subjects. This is illustrated in Fig. 6a—d which shows the computer-calculated distributions of C.I for both right and left quadrants and octants. In Fig. 6a (subject JSC) all the corresponding left and right field distributions are reasonably symmetrical with respect to each other, but for the other subjects (Fig. 6b—d) the distributions are often decidedly asymmetrical. Figure 6b shows the C.I distributions for the same subject as in Fig. 5, but for the larger stimulus field. The corresponding distributions of C.I are basically similar for the two cases although greater amplitudes were obtained with the larger field.

For three subjects (Fig. 6a—c), distinct differences were found in the form of the horizontal and vertical octant distributions for the upper field whereas the two lower octant distributions were generally more similar. These variations, which appear to be responsible for the difference between the upper and lower quadrant distributions, appear basically similar to those already described for subject DAJ in Fig. 5. For the fourth subject (SH) the distributions for two quadrants (right upper and left lower) seemed to fit the general pattern but those of the other two quadrants did not (Fig. 6d).

The additive relationship between half-field and quadrant distributions of C.I is well illustrated in Fig. 7. Here, there is a close correspondence between the half-field distributions and the sum of those for the constituent quadrants in each case. This suggests that the sources of C.I of the different quadrant VEPs are

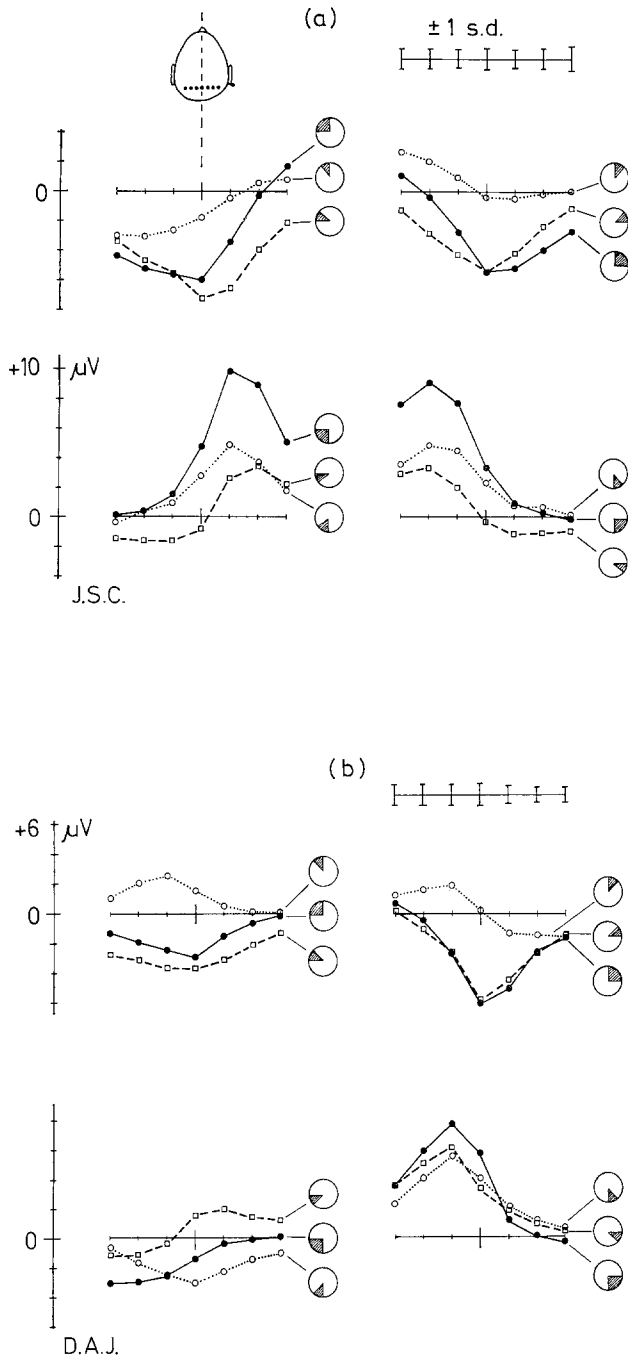
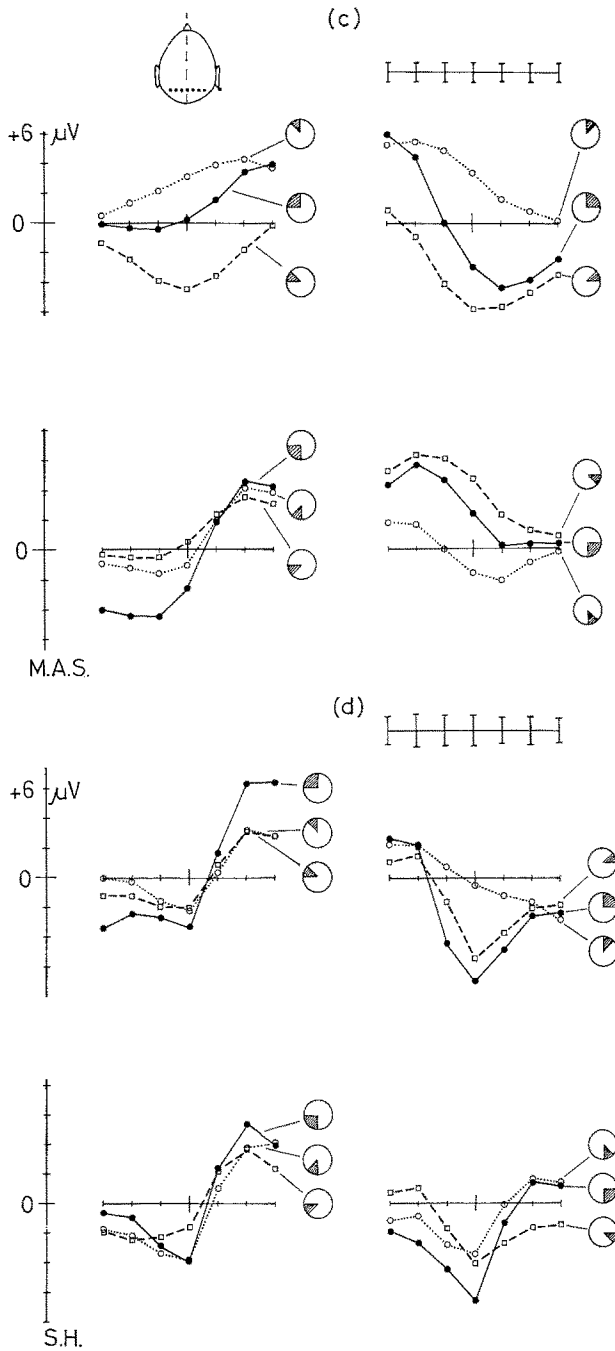


Fig. 6a-d. *Transverse amplitude distributions of C.I. for quadrant and octant stimuli in 4 subjects. Computer-calculated distributions of C.I. to stimulation of all quadrants (—) and horizontal (- - -) and vertical (. . .) octants. ± 1 s.d. bars for the corresponding electrode positions are shown in the upper right corner of each figure. For explanation see text*



independent. The results illustrated in Figs. 5 and 6 also indicate that in most, but not all cases, there is a fairly close correspondence between the shapes of the C.I. distributions of the quadrant VEPs and those of the sum of the appropriate octant VEPs. This additive property between responses to constituent parts of the sti-

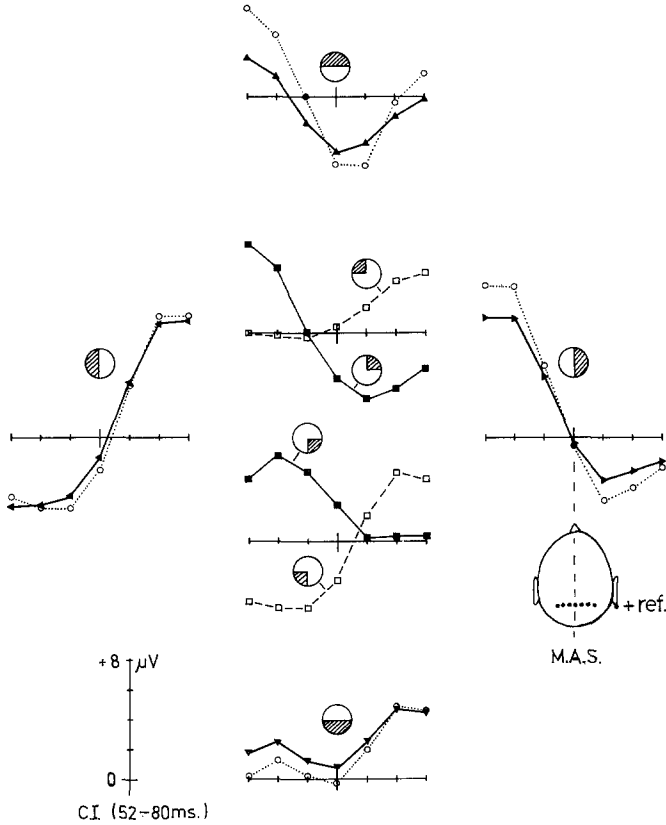


Fig. 7. *Summation of quadrant field distributions for C.I (52—80 msec).* Transverse distributions of C.I for right (■ — ■) and left (□ — □) quadrant stimulation are shown in the centre of the diagram. Half-field distributions (—) are compared with the sum of the appropriate quadrant distributions (· · ·) in the periphery. There is a close similarity in the form of the half-field distributions with those of the sum of the appropriate quadrants. The left and right half-field distributions have a clearly bipolar form, reversing polarity near the midline

mulus field may well be less precise when smaller areas are used, because the addition of extra boundary contours becomes proportionally more important. (Interestingly, we found a better correspondence between half-field distributions and the sum of the relevant quadrant distributions for a given subject when the stimulus pattern was an array of isolated squares than when a chequerboard pattern was used.)

Figure 7 also illustrates how the basic difference in form between the upper and lower and the left and right half-field distributions of C.I results from the different upper and lower quadrant distributions. The resulting upper and lower half-field distributions are both monopolar, of opposite polarity, whereas those of the left and right half-fields are bipolar and of opposite polarity. Although detailed component distribution studies have been carried out so far with only four subjects, it appears from visual inspection of the VEPs obtained in the earlier studies that these basic characteristics of C.I are typical of the majority of sub-

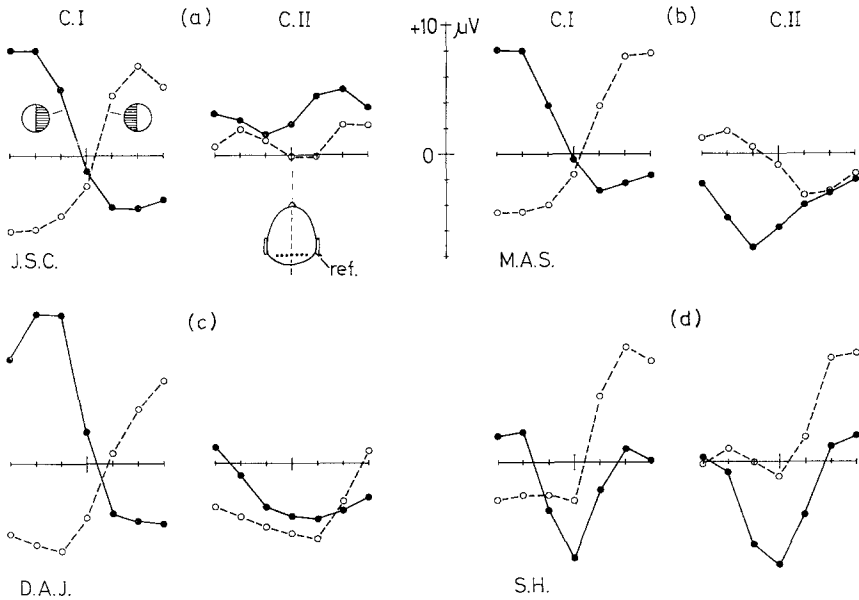


Fig. 8. Left (---) and right (—) half-field distributions of C.I and C.II for 4 subjects. For three subjects, the transverse distributions of C.I have complementary bipolar forms for left and right half-field stimulation whereas the corresponding distributions for C.II do not

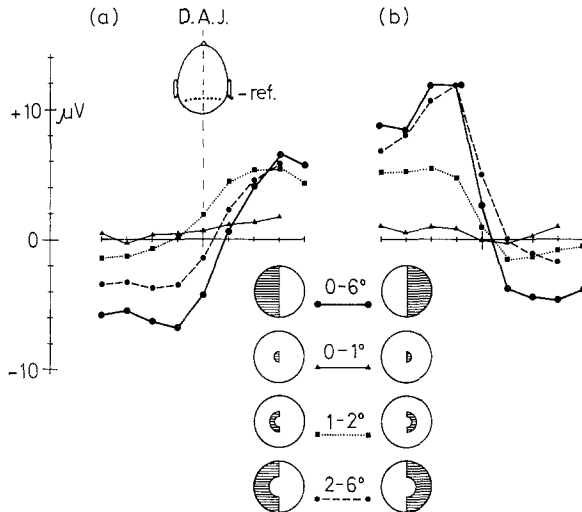


Fig. 9. Contribution of different annular regions of the left and right half-fields to the C.I distributions. The transverse distributions are shown for stimulation of the 0-1°, 1°-2°, 2°-6°, and the full 0-6° regions of the left and right half-fields. There is little contribution to the half-field distributions from the central 1° of the field, most of the response appearing to come from the 2°-6° region of the field

jects. The notable exception, of those so far tested, is subject SH. This is seen, for example, in Fig. 8, where the left and right half-field distributions of C.I are both bipolar in form for the other three subjects, but not for subject SH.

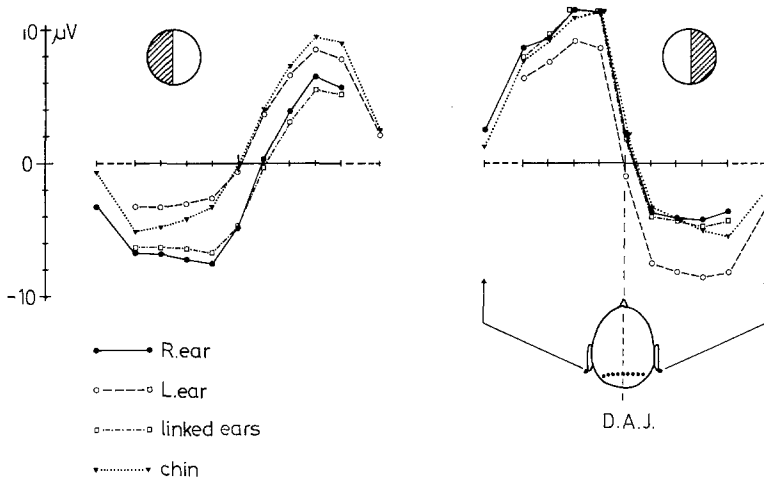


Fig. 10. Comparison of transverse distributions of C.I for different reference electrodes. The left and right half-field distributions of C.I are shown for left and right and linked ear references, as well as a chin reference. The shape of the distribution is more-or-less independent of the chosen reference electrode but its amplitude with respect to the baseline does change for the different references. The potential difference recorded between the two ears shows that the earlobe is not at zero potential

Figure 8 also demonstrates that, for the first three subjects, but not SH, the left and right half-field distributions of C.II do not have the bipolar form of those for C.I. This is because the C.II distributions of adjacent upper and lower quadrants are of opposite polarity and, unlike those of C.I, are fairly symmetrical with respect to each other (see Fig. 5), thus tending to cancel.

The major contribution to the component C.I comes from the area between 2° and 6° of the stimulus field. This is illustrated in Fig. 9 which shows the C.I distributions for different annular and disc regions of the left and right half-field. There is very little contribution from the central 1° of the field.

Control Experiments

A number of control experiments showed that the validity of these findings was not affected by the following experimental parameters:

1. Reference Electrode

Different reference electrodes were found to give small shifts of the transverse distribution, but did not alter their general shapes. Figure 10 shows the left and right half-field distributions of C.I for reference electrodes on the right, left and linked earlobes, and on the chin. Where appropriate, the responses actually present on each ear are also shown.

2. Luminance Changes

Control experiments in which the stimulus pattern was well defocussed were carried out routinely for all subjects and showed that these responses were pattern-specific and not related to any overall luminance change.

3. *Form of Pattern*

The observed VEP distributions were found to be independent of the spatial form of the pattern.

4. *Stimulus Sequence and Timing*

A comparison was made between the VEPs produced by two different pattern stimuli when (a) these VEPs were obtained in separate single stimulus runs (as in the experiments reported in this paper), and (b) when the two patterns were presented in a random order during the same averaging run. The VEPs obtained to the same stimulus when presented periodically and aperiodically were also compared. No significant differences were found for the characteristics of these pattern-specific components in either case. However, aperiodic stimulation was always used to reduce the effects of synchronization with any intrinsic EEG rhythm or "afterdischarge" of the VEPs. To achieve this the range of (random) variation of interstimulus periods was made longer than one alpha cycle.

Discussion

These studies of individual component distributions have clearly demonstrated the great influence of retinal location on the transverse amplitude distributions of C.I, and have shown that, on the basis of their surface distributions, C.I and C.II are separable components of presumably different origin.

How then do these variations in distribution of the VEP components relate to the structure and organization of the visual cortex? In an attempt to answer this question, we shall first of all briefly review what is known about the layout of the striate (primary) cortex and its retinotopic organization, and secondly consider the available information on the generation and transmission of cortically produced potentials fields. Then, we shall introduce a simple model derived from these considerations and show how our experimental observations of C.I, but not C.II, are predicted by this model. Finally we shall discuss the limitations of the model.

There have been a number of detailed studies of the retinal representation in striate and extrastriate regions of the visual cortex in cats (Talbot and Marshall, 1941; Bilge *et al.*, 1967; Hubel and Wiesel, 1967) and monkeys (Daniel and Whitteridge, 1961; Cowey, 1964; Cragg, 1969; Zeki, 1969) but only a few rather imprecise studies of retinal mapping in human striate cortex (Holmes, 1945; Teuber *et al.*, 1960; Brindley and Lewin, 1968). The scheme proposed by Holmes (1945, p. 352) for the retinotopic organization of the human striate cortex is however basically consistent with the results of the more precise animal experiments.

The striate cortex representing all but the very central part of the visual field is generally buried on the inner surfaces of the hemispheres, in and around the calcarine fissures, with a systematic relationship between progressively deeper cortical regions and increasingly eccentric areas of the field. It appears that the upper and lower field quadrants are represented in striate cortical regions respectively, below and above, the contralateral calcarine fissures, with an orderly mapping from the horizontal meridian representation, deep inside the fissures, to the vertical meridian representation on the medial surfaces (along the boundary

of striate and adjoining extrastriate cortex). On this basis, each horizontal field octant is represented chiefly within the calcarine fissures and the vertical octants chiefly on the medial surfaces.

The central part of the visual field is represented in the small, interindividually variable, proportion of striate cortex exposed on the outer surfaces near the occipital lobes (Polyak, 1957). (The results of mapping experiments in monkeys (Daniel and Whitteridge, 1961; Cowey, 1964) which showed that the considerably greater proportion of exposed simian striate cortex represents only a very limited area of the central visual field, suggest that the exposed human striate cortex probably represents no more than the central 1° or 2° in most cases.)

The gross electrical characteristics of the brain are as yet ill-defined. However, there is much evidence to suggest that, at least to a first approximation, the cortical generators of surface potential fields can be considered in terms of equivalent dipole sheets (Kelly *et al.*, 1965; Fourment *et al.*, 1965; Jami *et al.*, 1968; MacKay, 1969; Vaughan, 1969; Vaughan and Ritter, 1970; Schneider and Gerin, 1970). Also, it seems that the brain and its covering layers of bone, scalp, etc., can be considered essentially as a volume conductor with surrounding layers of different conductivity (Geisler and Gerstein, 1961; Paicer *et al.*, 1967; Rush and Driscoll, 1969; Vaughan, 1969; Vaughan and Ritter, 1970). (See Regan (1971) for a more detailed discussion of this problem.) Vaughan (1969) reported the successful use of a five-sphere isotropic volume conductor model of the brain in studies of the surface distributions of the major biphasic components (about 100–200 msec) of auditory, somesthetic and visual (flash) VEPs. He claimed that these VEP distributions conformed in each case with the surface potential fields produced by equivalent potential generators (dipole sheets) in the model, having configurations corresponding to those of the respective primary cortical regions. Using a pattern reversal stimulus Michael and Halliday (1971) have also attempted to relate surface VEP distributions to a cortical dipole model.

Let us assume that the arrangement of the striate cortex around the calcarine fissures and the interhemispheric gap is near symmetrical, and that these fissures are single furrows perpendicular to the (vertical) medial surfaces. Each quadrant is thus represented by a portion of striate cortex of right-angled transverse cross-section, whose horizontal and vertical 'arms' represent the horizontal and vertical octants of the visual field, respectively. Because of the inverted orientations of the regions of cortex on opposite sides of either the interhemispheric gap or the calcarine fissures, the potential fields associated with such regions will tend to cancel. Thus the potential fields produced to stimulation of the left and right half-fields will arise mainly from the contralateral medial portions of striate cortex. Similarly, the potential fields produced by upper and lower half-field stimulation will originate mainly in the cortical regions forming the 'floor' and 'roof', respectively of the two calcarine fissures. (For full field stimulation there will be little or no resultant potential field.)

If the cortex is considered as a dipole sheet within a volume conducting brain, the equivalent dipole axis for the cortex on the medial surfaces is parallel to the overlying surface row of electrodes. In this case the surface potential distribution will be bipolar, reversing polarity at the midline (Brazier, 1949). In contrast, the equivalent dipole axis for the cortex within the calcarine fissures is perpendicular

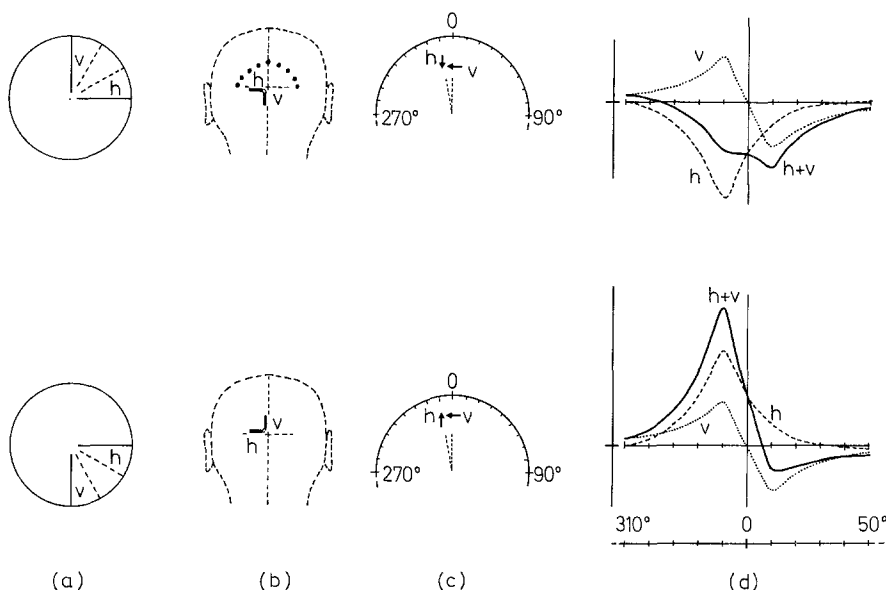


Fig. 11. Schematic arrangement and simple dipole model of the regions of striate cortex representing upper and lower quadrants of the visual field. The right upper and lower quadrants (a) are represented in transverse cross-section, by right-angled sheets of cortex (b), whose horizontal and vertical arms represent, respectively, the horizontal and vertical octants of the visual field. In (c) these cortical sections are represented by pairs of perpendicular dipoles of appropriate location and orientation. The surface potential distributions associated with these dipoles are shown in (d). (These distributions have been calculated from the formulae of Shaw and Roth (1955), where in this case, the depth of each dipole is $0.75R$, R being the sphere radius.)

The basic forms of these potential fields can be seen to be similar to the distributions of C.I for stimulation of the corresponding regions of the visual field (Fig. 5)

to the electrode row, so giving rise to monopolar distributions with maxima at the midline.

Thus, this dipole sheet model of the striate cortex predicts bipolar surface distributions (of opposite polarity) for left and right half-field stimulation, and monopolar distributions (of opposite polarity) for upper and lower field distributions. It can be seen that the half-field distributions of C.I shown in Fig. 7 show exactly these characteristics, corresponding in polarity to *surface-negative* dipole sheets.

The observed variations of the upper and lower quadrant and octant distributions of C.I can also be explained by this schematic arrangement of striate cortex. As a first approximation to the right-angled dipole sheets (Fig. 11b) representing the right upper and lower quadrants, Fig. 11c shows pairs of eccentric perpendicular dipoles of corresponding location and orientation, inside a sphere of homogeneous conductivity. The surface fields associated with such pairs of dipoles are shown in Fig. 11d, and this illustrates how the inversion of the monopolar potential field of the perpendicular dipole in the two cases (corresponding to the 'floor' and 'roof' of the calcarine fissure) produces basically different fields. The differences in distribution for the models of the right upper and lower qua-

drants and octants for surface negative dipoles can be seen to be essentially similar to those observed for the appropriate distributions of C.I in Fig. 5 and 6.

These findings suggest that the major part of C.I originates in striate cortex from surface negative activity. The striate cortical origin of C.I is supported by findings which show that there is very little contribution to this component from stimulation of the central 1° or so of the visual field (Fig. 9), the region which might be expected to be represented on the external lobe surfaces.

The schematic arrangement of striate cortex adopted in our model (Fig. 11 b) is almost certainly an oversimplification for most subjects. It is well known that there is considerable interindividual as well as interhemispheric variability in the layout of the striate cortex in and around the calcarine fissures, as well as in the layout of the fissures themselves. For example, Polyak (1957) states that "the configuration of the calcarine fissures shows almost an infinity of individual variation of *essentially the same sulcal and gyral pattern*". We have very little information on the degree of variability of this basic "sulcal and gyral pattern", but illustrations of transverse striate cortical sections in various textbooks and papers suggest that the general scheme adopted in the model is a reasonable first approximation of the striate cortical layout in many, although not all, hemispheres. They also indicate that in most cases the relative orientations of the cortical regions on the 'roof' and 'floor' of a given calcarine fissure and on the medial surface, are fairly consistent.

Such interindividual and interhemispheric variations in striate cortical topography could thus explain how most, but not all, subjects (hemispheres) show similar basic features of VEP distribution with retinal location, consistent with those predicted by the simple model. They could also explain the observed interindividual variation of left-right symmetry of the quadrant and octant C.I distributions.

The two-dipole model (Fig. 11 c) used to represent a right-angled sheet of cortex is, of course, also a gross oversimplification. However, it is intended only to demonstrate how the changes in orientation of the appropriate regions of striate cortex can explain the observed changes in *polarity* and in the basic *shapes* of the C.I distributions with retinal location. It is thought that these 'qualitative' conclusions made from the dipole model also hold for the case of a more realistic model, which takes into account the effects of the overlying layers of different conductivity, and the finite extent of the dipole sheet. Both factors tend to broaden or 'smear out' the surface distributions, a feature which probably helps to explain why the observed distributions are more widespread than may appear justified from the dimensions of the cortex. Other factors which have been neglected in this simple treatment include the effects of small cortical convolutions, particularly at the posterior extremities of the calcarine fissures, and possible inhomogeneities in the conductive properties of the brain. (See Regan (1971) for a more detailed discussion on the validity of dipole models.)

The choice of reference electrode is very important in the study of dipole-like fields (Fourment *et al.*, 1969; Jami *et al.*, 1968; Goff *et al.*, 1969; Kooi *et al.*, 1971; Michael and Halliday, 1971). No reference is truly 'indifferent', since each measurement is really evaluating the potential difference between two points in the dipole potential field. For dipole sources, the best reference would appear to be located

on or near the zero potential surface (a plane through and perpendicular to the dipole). Such a choice may not always be possible for multiple dipole sources.

In the present study an earlobe reference was used. This lies roughly on the zero-potential plane of the vertically oriented dipoles in the calcarine fissures, but is not so suitably placed for the horizontally oriented dipoles on the medial surfaces. However, Fig. 10 shows that the chin, right and left and linked ear references do not give significantly different results, thus indicating that all three reference points must lie on nearly equipotential surfaces for all the dipole sources considered. Note that in Fig. 10 the small responses measured on the two ears with respect to the chin, for left and right half-field stimulation are compatible with the proposed dipole sources on the medial surfaces.

Figure 10 shows that the basic shapes of the left and right half-field distributions are more-or-less independent of the choice of reference electrode. (However, the amplitude at any point on the distribution with respect to the baseline does vary with reference position, and there is seen to be a potential of 2—3 microvolts between the two ears). This indicates that any asymmetry noted in the *shape* of transverse distributions of C.I for left and right half-field or quadrant stimulation does not result from the choice of the right earlobe as the reference. Rather, it appears to be due to genuine cortical asymmetries.

Conclusions

These studies of the transverse distributions of the VEPs to the sudden brief presentation of a pattern in place of a continuously illuminated field, provide evidence for the spatially separate source locations of the first two components (C.I and C.II) of these responses. The basic features of the distribution of C.I, but not C.II, conform with the surface potential fields of an equivalent dipole sheet having the spatial configuration of the striate cortex. We therefore propose that the sources of C.I, but not C.II, lie in striate cortex.

The results described in this and the following paper clearly illustrate the great influence of retinal location and provide further evidence of the major importance of cortical topography in determining the characteristics of pattern-specific VEP components. We suggest that these experimental parameters may be of greater significance in the design and interpretation of other forms of VEP experiments than has hitherto been realised.

These findings also demonstrate the advantages of simultaneous multichannel investigations of surface VEP distributions over studies in which the VEPs are recorded from a few isolated scalp positions. They indicate a greater consistency in the *shapes* of the surface distributions than in their actual amplitudes, which are more susceptible to the influence of baseline variations, or to the choice of reference electrode.

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