J. Physiology (1985), **360**, *pp.* 233–246
With 1 *plate and* 4 *text-figures*
Printed in Great Britain

LOCALIZATION OF VISUALLY EVOKED CORTICAL ACTIVITY IN HUMANS

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(*Received 1 May 1984*)

SUMMARY

1. The locations of cortical activity evoked by visual stimuli presented at different positions in the visual field are deduced from the scalp topography of visually evoked potentials in humans.

2. To accomplish this, the Laplacian evoked potential is measured using a multi-electrode array. It is shown that the Laplacian response has the following useful attributes for this purpose. It is reference-free. Its spatial resolution is approximately 2 cm referred to the surface of the cortex. Its spatial sensitivity characteristic is that of a spatial band-pass filter. It is relatively insensitive to source–sink configurations that are oriented tangentially to the surface of the scalp. Only modest assumptions about the source–sink configuration are required to obtain a unique inversion of the scalp topography.

3. Stimuli consisting of checkerboard-filled octant or annular octant segments are presented as appearance–disappearance pulses at sixteen different positions in the visual field in randomized order. The locations of evoked cortical activity in the occipital, parietal and temporal lobes are represented on a Mercator projection map for each octant or octant segment stimulated.

4. Lower hemifield stimuli activate cortex which lies mainly on the convexity of the occipital lobe contralateral to the side of stimulus presentation in the visual field. The more peripheral the stimulus is in the visual field, the more rostral is the location of the active cortex. The rostral-to-caudal location of the evoked activity varies from subject to subject by as much as 3 cm on the surface of the occipital cortex. Furthermore, in any single subject there is a substantial amount of hemispheric asymmetry.

5. Upper hemifield stimuli activate cortex that lies on the extreme caudal pole of the occipital lobe. This activity is relatively weak, and in some subjects it is almost unmeasurable. It is suggested that the representation of the upper hemifield in the cortex lies mostly on the inferior and mesial walls of the occipital lobe and possibly within the calcarine fissures. Those locations are inaccessible to the Laplacian analysis because the current generators therein may be oriented tangentially to the surface of the overlying scalp.

6. Posterior parietal lobe activity and/or inferior temporal lobe activity is frequently evoked. Different subjects have different patterns of evoked activity.

Unilateral or bilateral posterior parietal lobe activity is the most common pattern. Unilateral inferior temporal lobe activity is a less common pattern. The evoked parietal and/or temporal lobe activity does not lateralize in relationship to the position of the stimulus in the visual field.

7. Posterior parietal lobe activity and/or inferior temporal lobe activity is most frequently observed when upper hemifield stimuli are used and it is often the predominant evoked cortical activity under these conditions. Evoked activity in these cortical areas may be masked by relatively strong activity on the convexity of the adjacent occipital lobe evoked by stimuli presented to the lower hemifield.

INTRODUCTION

In the study reported herein, the scalp topography of the visually evoked potential (v.e.p.) in humans is used to deduce the locations of activity in the cerebral cortex evoked by stimuli presented at various different positions in the visual field. Previous studies with similar intent have produced conflicting results (Jeffreys, 1969; Vaughan, 1969; Halliday & Michael, 1970; Jeffreys, 1971; Michael & Halliday, 1971; Jeffreys & Axford, 1972*a*, *b*; Lehman, Meles & Mir, 1977; Jeffreys & Smith, 1979; Lesevre & Joseph, 1979; Darcey & Fender, 1980). Several factors may have combined to cause these conflicting results. The first factor concerns the way in which v.e.p.s were frequently recorded. A so-called monopolar electrode placement ('derivation') was often used in which the potential difference was measured between one electrode on the scalp ('active' electrode) and another often placed on an ear or mastoid ('reference' or 'indifferent' electrode). However, under these recording conditions the dimension of the brain region causing the v.e.p. was likely to have exceeded 2·5 cm (see Theory below) so that no electrode can be safely assumed to be indifferent to the evoked brain activity. The second factor concerns the relationship of the scalp topography of the v.e.p. to the geometry of the sources and sinks of electrical current in the brain that cause it. Since the passive properties of the human head are well approximated by a linear model (Wilson & Bayley, 1950; Geisler & Gerstein, 1961; Rush & Driscoll, 1968; Rush & Driscoll, 1969; Hosek, Sances, Jodat & Larson, 1978; Kavanagh, Darcey, Lehman & Fender, 1978), a measured scalp topography can result from an 'infinite' number of source–sink configurations. This problem (no unique solution for inversion of scalp topography) follows directly from the principle of linear superposition. In practice, one must make initial assumptions about the source–sink configuration that are sufficient to limit the solution. However, if the assumptions are restrictive, experiments simply test them and provide little or no information outside this rigid framework. Many studies assumed the source–sink configuration implied by the cruciate anatomy of the striate cortex. Alternatively a severely reductionist approach was taken in which the source–sink configuration was reduced to that of an 'equivalent' dipole (Henderson, Butler & Glass, 1975). Although not intuitively obvious, the electrode derivation used to obtain the topographical data has an important bearing on the required initial assumptions (see Theory below). The third factor concerns the variability of the anatomy of the human visual system. The exact position of the striate cortex varies appreciably in normal human brains (Brindley, 1972) and this implies a similar variation for the position of immediately adjacent extrastriate cortex. Previous studies were not prepared to address this problem. The last factor concerns the effect of evoked activity in the posterior parietal and the inferior temporal cortices, these areas being known to be involved in the processing of visual information in humans and in non-human primates (Motter & Mountcastle, 1981; Mountcastle, Anderson & Motter, 1981; Hyvärinen, 1982; Milner, 1968; Gross, 1973; Rolls, Judge & Sanghera, 1977; Ridley, Hester & Ettlinger, 1977; Gross, Bender & Gerstein, 1979; Mikami & Kubota, 1980; Fuster & Jervey, 1982). Previous studies were not flexible enough to deal with the possibility that the scalp topography of the v.e.p. might have reflected activity from these brain areas.

Thus the problem of deducing cortical localization from v.e.p. topography demands not only a reference-free electrode deviation, but also one that permits the initial assumptions about source–sink configuration to be relaxed sufficiently to assure a flexible approach to interpretation. These requirements can be met by using the Laplacian derivative of the v.e.p., $\nabla^2 V$, defined as,

$$\nabla^2 V = \frac{\partial^2 V}{\partial X^2} + \frac{\partial^2 V}{\partial Y^2}, \tag{1}$$

where V is the v.e.p., an implicit function of time and position on the scalp (x, y). (Scalp position can be given in Cartesian coordinates without serious error because only small distances need to be considered in eqn. (1).) Eqn. (1) shows that $\nabla^2 V$ is reference-free. It is a measure of the curvature of potential field on the scalp. It is easily shown that $\nabla^2 V$ is also a measure of the component of electrical current flowing normal to the surface of the scalp and as such it rejects gradients of potential that can be caused by sources or sinks of electrical current in the brain at locations relatively remote from the point at which it is measured. The Laplacian response has been used to aid in the localization of epileptogenic foci in humans from electroencephalograms (Hjorth, 1976; Wallin & Stalberg, 1980), and some discussion of its general properties with regard to the electroencephalogram has peviously appeared (Nunez, 1981). It has been used to study event-related potentials (Mackay, 1984). Its properties are explored in greater detail below.

METHODS

Theory

The Laplacian response can be conveniently estimated using five active electrodes arranged in the form of a cross on the scalp, with outer electrodes equispaced by a distance D from the centre electrode (see Fig. 1, insert). From this derivation, the sum of orthogonal second differences in the potential field of a small region of the scalp is obtained. Let e_0 be the potential at the centre electrode, e_1 and e_2 the potentials at the outer electrodes along the coronal arc, and e_3 and e_4 those at the outer electrodes along a sagital arc. Then,

$$\nabla^2 V \cong [(e_1 - e_0) - (e_0 - e_2)] + [(e_3 - e_0) - (e_0 - e_4)]$$

and

$$\nabla^2 V \cong e_1 + e_2 + e_3 + e_4 - 4e_0. \tag{2}$$

All potentials are measured relative to an arbitrary electrode (ground electrode) whose placement has no effect on the estimate since its potential entirely drops out of eqn. (2).

The three-concentric-sphere model of the human head (Rush & Driscoll, 1969; Hosek *et al.* 1978; Kavanagh *et al.* 1978) was used to quantitatively explore the properties of the Laplacian estimator described above. The brain, including the cerebrospinal fluid and meninges was represented by a sphere 7·85 cm in radius, the skull by a shell with outer radius 8·47 cm, and the scalp by a shell

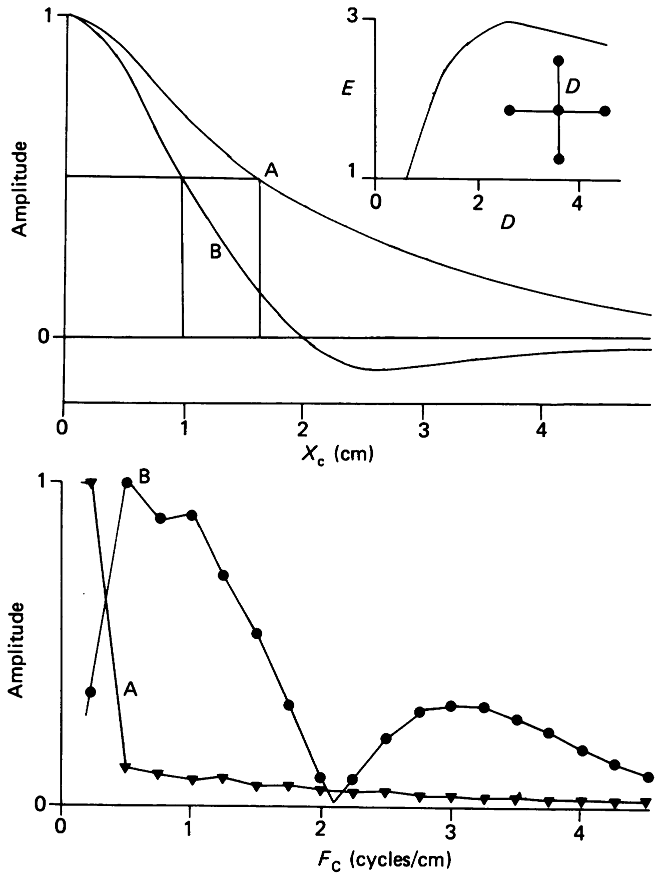

Fig. 1. Top: relationship of amplitudes of conventional v.e.p. (A) and Laplacian response (B; $D = 2{\cdot}5$ cm) to location (X_c) of radially oriented unit dipole in cortex calculated from three-concentric-sphere model. $X_c = 0$ means that the unit dipole lies on the same radius as the centre electrode of the Laplacian electrode derivation or the active electrode of conventional v.e.p. Half-amplitude points indicated. Each curve (A and B) is separately normalized. Top insert: configuration of Laplacian electrode derivation. Filled circles: electrode locations, D = outer-to-centre-electrode spacing (cm). Top insert: relationship of E (ratio amplitude of Laplacian response to half-amplitude width) to D. Bottom: relationship of amplitude of Fourier transform of surfaces specified by curves in top to spatial frequency (F_C, cycles/cm on surface of cortex) for conventional v.e.p. (A) and Laplacian response (B; $D = 2{\cdot}5$ cm). Amplitudes top and bottom normalized to maximum value. To obtain surfaces that fully characterize the relationships (top and bottom) rotate curves 360 deg about the Y axis.

with outer radius 9·20 cm. The conductivity of brain and scalp, assumed isotropic and homogeneous, were taken as 80 times greater than that of the skull (Rush & Driscoll, 1969; Nunez, 1981).

The intrinsic spatial resolution of the Laplacian derivative was estimated by calculating its response amplitude to a radially oriented unit magnitude dipole just under the surface of the cortex as a function of the location of the dipole on the cortical mantle, and this was compared to the response amplitude of the centre electrode *vs.* a (phantom) electrode at infinity (conventional v.e.p.) (see Nunez, 1981, p. 461 for the formulae used to calculate these). Fig. 1, top, shows the results. Each curve shown therein is the half-profile of a surface which is rotationally symmetrical about the Y axis. The half-amplitude width of the profile for the conventional v.e.p. (A) is 3·3 cm, i.e.

±1·65 cm. For values of X_c greater than 6·2 cm, the curve gradually approached zero. The half-amplitude width of the profile for the Laplacian estimator with $D = 2·5$ cm is 2·0 cm (B), i.e. ±1·0 cm. The more prominent negative tail of this curve also gradually approached zero.

Both the half-amplitude width and the maximum amplitude of the Laplacian response increase as D increases. Let E be the ratio of maximum amplitude response to half-amplitude width. It is a convenient measure of the over-all efficiency of the Laplacian response. Fig. 1, top, insert shows that E increases sharply with increasing values of D, reaches a peak at 2·5 cm and thereafter decreases as D increases. It follows that $D = 2·5$ cm is an optimum value for the spacing between the centre and outer electrodes.

The surface representing the spatial response of the Laplacian derivative has a 'Mexican hat' shape, while that representing the conventional v.e.p. is nearly monotonic. A better understanding of the implications of this difference can be had from the spatial frequency domain representations of the surfaces, where spatial frequency is measured in cycles/cm on the surface of the cortex. Fig. 1, bottom, shows the results obtained by Fourier transformation. The amplitudes of the Fourier transforms are surfaces with rotational symmetry about the Y axis and the half-profiles (Fig. 1, bottom) specify the surfaces. The properties of the conventional v.e.p. (A) approximate those of a low-pass filter with half-amplitude cut-off at 0·4 cycles/cm. Thus, the conventional v.e.p. responds best to regions of active cortex that exceed 2·5 cm in dimension. The properties of the Laplacian derivative (B; $D = 2·5$ cm) approximate those of a band-pass filter with half-amplitude cut-offs at 0·32 and 1·56 cycles/cm. Thus the Laplacian derivative responds best to regions of active cortex 0·6 to 3·1 cm in dimension. (The subsidiary peak near 3 cycles/cm (B) extends the sensitivity to slightly smaller regions.) These are useful properties in that the Laplacian derivative rejects α activity which is well known to synchronously involve relatively large areas of cortex, and it also rejects possible perturbations in the potential field on the scalp attributable to the convolutions of the cortex.

The two representations of the spatial sensitivity of the Laplacian derivative shown in Fig. 1, one in the spatial and the other in the spatial frequency domain are linked by the Gabor theorem (Gabor, 1946) which states that the products of the widths of the two surfaces must exceed a physical constant. In this sense, an optimum spatial profile exists. A spatial profile that is narrower than optimum produces side lobes in the spatial frequency domain. Surface B of Fig. 1, top, is in fact slightly narrower than optimum and this causes the side lobe near 3 cycles/cm in the frequency domain representation.

The three-concentric-sphere model was also used to calculate the response amplitude to a tangentially oriented unit magnitude dipole just under the surface of the cortex as a function of its location on the cortical mantle, for both the Laplacian derivative and conventional v.e.p. The Laplacian response ($D = 2·5$ cm) was found to be largest when the tangential dipole was displaced 2·0 cm from just under the centre electrode, at which location the amplitude was approximately 9% of that caused by a radial dipole just under the centre electrode. The response of the conventional v.e.p. was largest when the tangentially oriented dipole was displaced 3·5 cm from just under the active electrode, at which location the amplitude was approximately 24% of that caused by a radial dipole just under the active electrode. Thus the Laplacian derivative is relatively insensitive to tangentially oriented dipole sources in the brain.

Because the spatial sensitivity of the Laplacian estimator has a 'Mexican hat' shape, the boundaries of regions of active cortex can be estimated from the zero-crossings of a montage of Laplacian outputs (Marr, 1966; Logan, 1977; Marr & Hildreth, 1980). It follows that iso-activity contours can be interpolated, and thus it is possible to construct a complete map specifying the activity of cortex underlying the montage with resolution determined by both the intrinsic resolution of the Laplacian response and the density of the Laplacian sample points.

It is well known that if one specifies the source–sink configuration of an electrical current generator in the brain, the scalp topography of the resulting potential field is uniquely determined, but that the inverse problem has no unique solution. As described in the introductory remarks above, an assumption that limits the solution must be made about the source–sink configuration in order to invert the scalp topography. When conventional 'monopolar' electrode derivations are used to measure the scalp topography the assumptions must be excessively restrictive. When the Laplacian derivative is used, the assumptions can be greatly relaxed to include only an assumption about the dimensions of the active regions of the brain that cause the v.e.p.

Procedure

The Laplacian response was estimated using eqn. (2) by constructing an analog device that implemented the operation specified therein. The device contained two separate channels and avoided the cumbersome requirement that ten active electrodes be simultaneously monitored. The resulting signals were amplified by a factor of 10^5, band-pass filtered between 1 and 50 Hz (3 dB points, 3 pole Butterworth filters) and digitized at 143 Hz for computer averaging (128 trials per average).

The stimuli were checkerboard pattern appearance–disappearance pulses, 16·7 ms in duration, containing 14 arc minutes black and white checks of high contrast. They were presented at regular intervals of 437 ms as octants 0–2 arc deg (central octants) or as annular segments of octants 2–6 deg (peripheral octants). Octant identification numbers are shown in Fig. 2. During the interstimulus interval the entire field (12 × 18 deg) was homogeneously illuminated at about 10 foot-lambert and the stimuli had the same space-averaged luminance as the field that each partly replaced. A fixation cross was always present. Subjects sat at 1 m from the display, and viewed it binocularly. They were instructed to maintain fixation on the cross.

The display was generated on a high resolution black and white computer-controlled video system with a 60 Hz frame rate (Grinnel System, San Jose, CA, U.S.A., 512 by 1024 pixels) with its own computer. A PDP 1134 computer (Digital Equipment Corporation, Maynard, MA, U.S.A.) controlled the display computer to synchronize the display to the experiment, and handled data acquisition and processing. An experimental run consisted of 128 presentations of each of the sixteen octants, with presentation order randomized in blocks of sixteen containing all possible octants. A recording session consisted of two runs. Subjects sat for one to eight sessions. Session to session variability was small and in some experiments results from different sessions were collated.

The electrodes were 8 mm gold cups. Care was taken to minimize the spread of electrode paste when they were applied to the scalp. In preliminary experiments no systematic differences were found between recordings taken with these electrodes and recordings taken with 4 mm disk electrodes. The smaller electrodes proved troublesome to keep attached to the scalp and were not used. It was also verified that 2·5 cm was the optimum electrode spacing for the Laplacian derivative. When the spacing was 1 cm, signal-to-noise ratio was degraded. When the spacing was 4 cm octant specificity was degraded. (See Fig. 2 for meaning of octant specificity.) Thus 2·5 cm was regularly used as the electrode spacing for the Laplacian derivative.

Some of the results are herein represented by maps showing the relative magnitude of evoked cortical activity as a function of location on the cortical mantle on a brightness scale (grey scale). This required the interpolation of magnitudes between actual data samples, a process that must be done cautiously to avoid spurious spherical harmonics (aliases) and to achieve the best possible estimate of the evoked activity surface that the data allows (Parker, Kenyon & Troxel, 1983). A perfect interpolating function would have the properties of an ideal low-pass filter, but practical considerations suggested the use of the derivative of the two-dimensional Gaussian distribution which was applied using the equation:

$$A(x,y) = \sum_{j} (1-r^2/2\sigma^2) \exp(-r^2/2\sigma^2)\, E_j, \tag{3}$$

where $A(x, y)$ = interpolated value at coordinate x, y
r = distance between the point to be interpolated and the jth Laplacian centre electrode location $\sqrt{(x-x_j)^2+(y-y_j)^2}$
E_j = amplitude of the Laplacian response at the jth centre electrode location
$2\sigma^2$ = 0·794 × (average distance between Laplacian centre electrode locations).

The summation in eqn. (3) is carried out over all Laplacian centre electrode locations, and all distances are referenced to the cortical mantle. The value of $2\sigma^2$ matched the half-amplitude width of the derivative of the two-dimensional Gaussian distribution to the average distance between Laplacian centre electrode locations as suggested by the sampling theorum.

The maps shown herein are all Mercator projections, i.e. the projection of the spherical cortical mantle onto a cylinder with tangency at the cortex just below 10–20 system location 0z, and the cylinder unfolded to a flat surface. As a result the top of each map is expanded 22 % horizontally relative to the equator.

RESULTS

Fig. 2 compares the conventional v.e.p. (02 *vs*. right mastoid, 10–20 system) to the simultaneously recorded Laplacian response with centre electrode at 02 for one subject. These have similar wave forms (see insert to Fig. 2), but there is a considerable difference between the octant specificities of the two responses, as shown by the relationships between the response amplitude (see insert for measurement) and the octant stimulated. Six subjects were studied in this way. The results shown in Fig. 2 are representative. The conventional v.e.p.s of some subjects contained oscillations near 10 Hz (presumably the intrusion of α activity) and for these subjects the Laplacian response had much less oscillation. Octant specificity of the Laplacian response was not systematically different when the amplitude measured was that of the trough alone, the peak alone, or the peak to trough. Octant specificity was the same for stimuli containing 51 arc minute checks, or for blank fields of 50 % contrast, or for monocular viewing as it was for binocular viewing and 14 arc minute checkerboard stimuli.

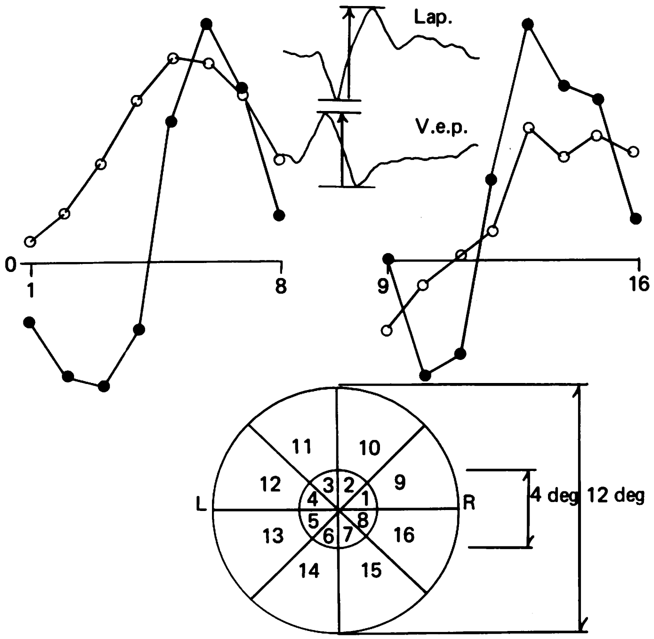

Fig. 2. Top: relationship of amplitudes of conventional v.e.p. (○) and Laplacian (●) to octant stimulated. Data for one subject, Laplacian response and v.e.p. recorded simultaneously. Conventional v.e.p.: 02 *vs*. right mastoid. Laplacian response: centre electrode at 02, $D = 2{\cdot}5$ cm. Top insert: wave form of Laplacian response (Lap.) and conventional v.e.p. for stimulation of octant 6. Laplacian response: upward deflexion, electrical current flowing normal to and into the scalp. V.e.p.: upward deflexion, 02 positive to mastoid. Amplitude measurements indicated. Bottom: octant numbering convention.

Fig. 3 shows representative Laplacian responses for one subject using centre electrode location 02. The wave forms are all relatively simple. The largest response consists of a prominent negative deflexion that forms a trough at about 110 ms after stimulus onset, followed by a prominent positive deflexion that peaks at about 170 ms after stimulus onset. (Smaller deflexions were not reliable.) Peaks and troughs occur at similar times for all octants, but amplitude and polarity are functions of the octant stimulated. In most of twenty subjects studied as above, the maximum response amplitude followed stimulation of octant 6, and in the remaining subjects it followed stimulation of octant 5. The greatest subject-to-subject variability occurred in the amplitudes of responses to peripheral octant stimuli. The records shown in Fig. 3 contain relatively large amplitude responses to peripheral octant stimulation.

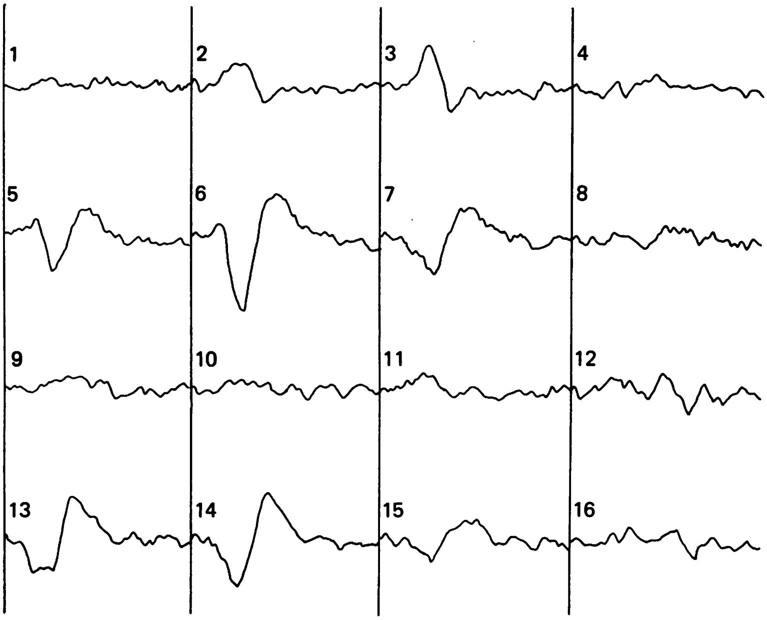

Fig. 3. Laplacian responses to stimuli in different octants. Each trace is the average of 128 responses and represents 420 ms following stimulus offset (vertical line at left extremity). Upward deflexion: electrical current flowing normal to and into scalp. Centre electrode location 02, $D = 2{\cdot}5$ cm. Number near each trace denotes the octant stimulated. All data from one subject and one experimental run.

In ten subjects the Laplacian response was recorded from fourteen different centre electrode locations spaced over the posterior scalp from the inion to Pz and from T5 to T6. A map showing the locations of evoked cortical activity was constructed for each octant and for each subject. Fig (4), top left, shows the fourteen centre-electrode locations used and labels those locations having standard 10–20 system names. Plate 1 shows the sixteen maps for one subject arranged so that those maps representing octants in the left visual hemifield are in the left half of the Figure, and those representing octants in the upper visual hemifield are in the top half. Stimuli presented in the right lower visual field evoke activity in the cortex left of the mid line near the equator. Stimuli presented in the left lower visual field evoke activity in cortex right of the mid line near the equator. This relationship, i.e. contralateralization, is clearest for the octants farthest from the vertical meridian. Some degree of bilateral cortical activity is evoked by octant stimuli adjacent to the vertical meridian, presumably due to the subject's imperfect fixation. Peripheral octant stimuli evoke activity in cortex that is located rostral to that activated by central octal stimuli, all stimuli being presented in the lower hemifield. Upper hemifield stimuli evoke much weaker activity than do lower hemifield stimuli by a factor to 4–10. (See numbers at lower right in each map which indicate maximum relative amplitude.) Some of this evoked activity occurs in the occipital lobe caudal to that evoked by lower hemifield stimuli and this evoked activity shows some degree of contralateralization. However, much of the activity evoked by upper hemifield stimuli occurs in the posterior parietal and inferior temporal cortex. During the experimental session this right-handed subject imagined that the fixation cross was an aircraft and that the stimuli were explosions of gunfire to be avoided.

TABLE 1. Average evoked cortical activity for upper hemifield stimuli

	Centre electrode location					
Subject	T5	P3	Pz	P4	T6	02 (maximum)*
J.X.B.	−65	0	13	−5	−24	390
R.K.C.	−30	−8	30	−9	8	163
S.A.G.	−45	9	41	7	−16	135
E.M.M.	38	0	−7	10	−48	132
K.X.R.	−57	−8	5	7	−34	320
C.M.S.	−58	46	−6	−16	−42	88
K.L.T.	−17	6	−3	10	24	120
E.E.W.	−144	2	88	−12	−39	127
A.L.H.	−39	1	3	5	8	167
J.L.F.	−25	14	2	4	−22	233

* The units in this Table are arbitrary. This column lists the maximum value recorded at 02 and reflects the response amplitude following stimuli presented in either octant 5 or 6.

In each map shown in Pl. 1, the bright ring or rings sketch the iso-activity contour lines associated with evoked activity whose magnitude is 50 % of maximum for that map. The 50 % contour lines regularly fall in regions of steep descent of activity magnitude, indicating that those cortical regions in which activity is evoked are all crisply defined. Thus the 50 % contour lines are good indicators of the locations of evoked activity and may serve to summarize a great many data conveniently. Fig. 4 shows a summary of results for all ten subjects made by overlaying the 50 % contours on a single map for each subject. Results are shown only for the lower hemifield stimuli. The first map is for the same subject whose data are shown in Pl. 1. While there is much variation from subject to subject, several features are consistent. The central lower hemifield octants (5–8) and the peripheral lower hemifield octants (13–16) evoke cortical activity that localizes progressively from the right to left hemisphere. Peripheral lower hemifield octants evoke activity more rostrally to that evoked by central ones. The over-all rostral-to-caudal location of the evoked cortical activity varies by as much as 3 cm from subject to subject. There is substantial hemispheric asymmetry in the locations of active cortex in most subjects, so that the areas of active cortex are frequently more rostral in one hemisphere than in the other.

The pattern of activity evoked by upper hemifield stimuli shown in Pl. 1 is representative of the results for all ten subjects studied. Predominant regions of cortical activity were regularly found in the posterior parietal and/or inferior temporal lobe. Table 1 shows how this activity distributed for each subject. In seven of the ten subjects central, left or right parietal lobe activity was the predominant locus of evoked cortical activity. In three of the ten subjects left or right temporal lobe activity was the predominant locus of evoked cortical activity.

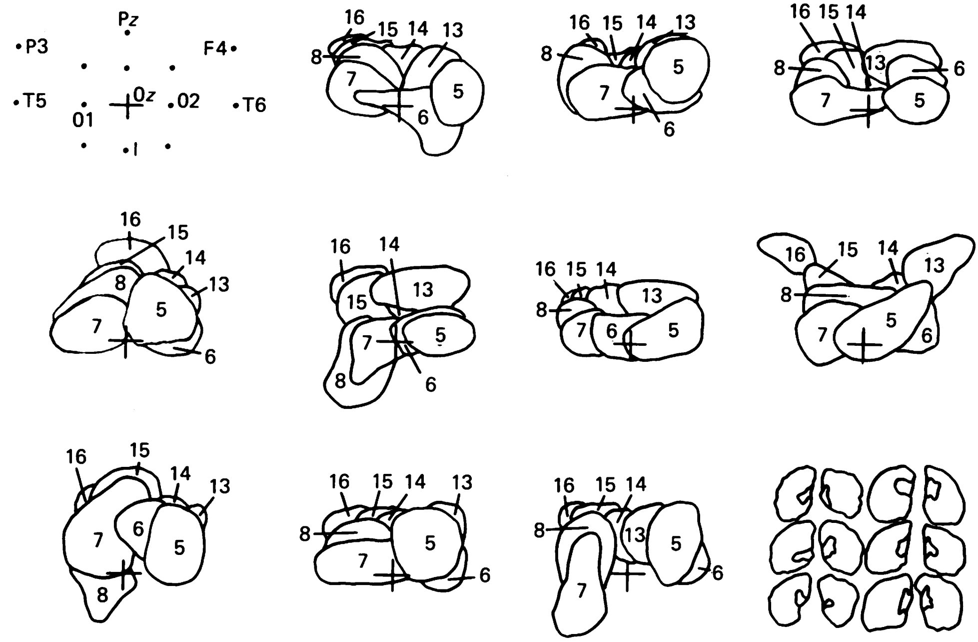

Fig. 4. Summary of results for ten subjects showing the loci of cortical activity evoked by lower hemifield stimuli. Each map, a Mercator projection as in Pl. 1, shows an overlay of the 50 % iso-activity contour lines for each subject. The cross marks the cortex just below 0z. The first map is for same subject whose results are shown in Pl. 1. Insert upper left: centre electrode locations. Insert lower right: projection of area 17 in six cadaver brains from Brindley (1972).

DISCUSSION

The results presented above are in reasonable agreement with theory as follows. At a particular position on the scalp, the specificity of the Laplacian derivative for the position of a stimulus in the visual field was substantially more discrete than that of the conventional v.e.p. The specificity was independent of that particular feature of the wave form of the Laplacian response which was chosen as a measurement criterion. The specificity was independent of stimulus attributes such as checksize or binocular *vs.* monocular viewing.

Maps of cortical activity constructed from a montage of Laplacian measurements contained several features consistent with known anatomy of the visual system, and with its variability in humans (Brindley & Lewin, 1968; Brindley, 1972). (1) Lower hemifield stimuli evoked activity on the convexity of the contralateral occipital lobe. (2) Peripheral lower hemifield stimuli evoked activity in cortex located rostrally to that evoked by central lower hemifield stimuli. (3) The rostral-to-caudal location of cortical activity evoked by lower hemifield stimuli varied by as much as 3 cm from subject to subject, and in a given subject hemispheric asymmetry was common. In these respects, Fig. 4 is remarkably similar to Brindley's (1972) pictures showing the location of striate cortex on the convexity of the occipital lobe in six cadaver brains (Fig. 4, inset). However, this does not imply that only striate cortex was activated, as the resolution of the maps was not adequate to distinguish striate from immediately adjacent extrastriate activity. (4) Upper hemifield stimuli either evoked weak cortical activity near the caudal pole of the occipital lobe, or evoked activity only in the posterior parietal and/or inferior temporal lobes. This suggests that the cortex representing the upper hemifield lies mostly on the inferior and mesial surfaces of the occipital lobe and within the calcarine fissure. As discussed in the Theory section above, these areas are inaccessible to the Laplacian derivative because the current generators contained therein are oriented tangentially to the scalp.

Activity in the posterior parietal lobe, either bilateral or unilateral, was often evoked, and activity in the inferior temporal lobe, usually unilateral, was sometimes evoked, especially in response to stimuli presented in the upper hemifields. When the activity was mostly unilateral, lateralization was not affected by the lateral position of the stimulus in the visual field. Studies of humans with brain lesions, as well as neurophysiological studies in non-human primates, suggest that the posterior parietal lobe is concerned with visual information related to spatial orientation, including compensatory processing for eye movements (Motter & Mountcastle, 1981; Mountcastle *et al.* 1981; Hyvärinen, 1982), and that the inferior temporal lobe is concerned with the identification of stimulus attributes such as colour and form and with the short-term visual memory (Milner, 1968; Gross, 1973; Rolls *et al.* 1977, Ridley *et al.* 1977; Gross *et al.* 1979; Mikami & Kubota, 1980; Fuster & Jervey, 1982). The subjects studied herein often invented games in which they engaged during the measurements that involved interpreting the stimuli with regard to shape and position in the visual field. This suggests a plausible basis for the variability of the posterior parietal and inferior temporal lobe activity that was found from subject to subject. Hemispheric lateralization related to cognitive processing may also have played some role in this regard.

Although posterior parietal and inferior temporal lobe activity was usually evoked when upper hemifield stimuli were used and was rarely evoked when lower hemifield stimuli were used, this need not imply that upper hemifield stimuli have a unique effect in this respect. Lower hemifield stimuli may have caused sufficiently strong activity on the convexity of the occipital lobe to mask parietal or temporal lobe activity. Masking can be readily understood by interpreting the Laplacian response as a measurement of the normal component of electrical current flow in the scalp. Assume that the initial events in the activation of a patch of cortex are excitatory post-synaptic potentials (e.p.s.p.s) on the apical dendrites of pyramidal cells near their cell bodies. This would give rise to a closed field (Klee & Rall, 1977) and so to electrical current flowing outward in the scalp over the patch of cortex. But the electrical current must return to a sink in the cortex through the surrounding scalp. Activation of a second patch of cortex under the scalp carrying the return current would cause current flow opposing the return current and mutual interference would result. If the activation of the second patch of cortex were much weaker than that of the first, its activity could be entirely masked. This model of cortical activation would explain the initial outward current flow in the scalp immediately above active cortex as seen in Fig. 2; as the activity evoked in the inferior temporal and posterior parietal lobe was usually much weaker under any stimulus conditions than that evoked by lower hemifield stimuli, masking of this type seems possible.

That the upper hemifield stimuli frequently evoked activity in the posterior parietal and/or the inferior temporal lobe that constituted the predominant evoked cortical activity and that did not lateralize in relation to stimulus position in the visual field, helps to rationalize the inconsistencies often found when conventional v.e.p.s were used to study scalp topography. And it suggests a plausible explanation for the frequent failures of conventional v.e.p. studies to detect hemianopsia and quadrantanopsia in neurological disease (Haimovic & Pedley, 1982; Blumhardt, Barett, Kriss & Halliday, 1982).

There are several probable sources of error inherent in the construction of the maps of cortical activity presented herein. (1) It is assumed that the conductivity of the scalp is homogeneous and isotropic so that no correction is applied to sum the orthogonal second differences of the scalp potential or to compare Laplacian responses at different scalp locations. (2) Non-homogeneities of skull conductance, such as might occur at sutures are neglected. (3) Unstable fixation clearly blurred cortical localization. Inasmuch as the central octant stimuli were relatively small, it would not take much instability to have an effect. (4) The centre-electrode to centre-electrode spacing of the montage of Laplacian derivatives was coarse compared to the latter's intrinsic resolution and limited the spatial resolution of the technique. This was to some degree a matter of expediency required to obtain the services of unpaid subjects reluctant to commit themselves to a protracted series of measurements.

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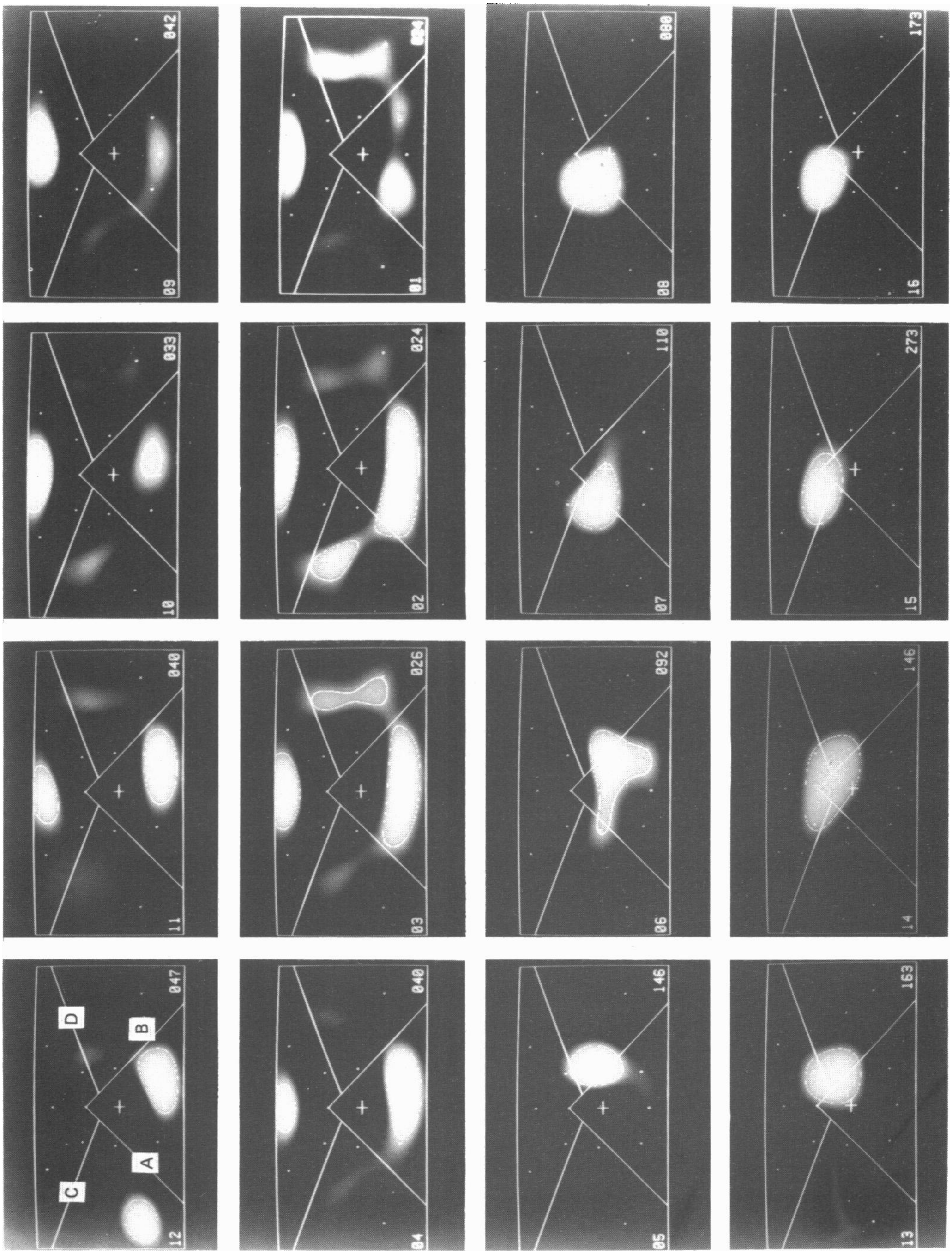
EXPLANATION OF PLATE

Cortical activity evoked by each of the sixteen octants stimulated (number at lower left) for one subject. Magnitude, shown by grey-scale level, normalized for each octant. Number at lower right equals maximum amplitude. Bright dotted rings show 50% iso-activity contours. Each map is a Mercator projection with equator through cross. Bright dots show projections of centre electrode locations onto cortex. Cortical landmarks (accuracy ±1 cm): A, left occipital–temporal lobe border; B, right occipital–temporal lobe border; C, left temporal–parietal lobe border; D, right temporal–parietal lobe border. Scale: vertical extent of each map 10·9 cm; horizontal extent at equator 20·6 cm.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