

THE LATENCY AND FORM IN MAN OF THE OCCIPITAL POTENTIALS EVOKED BY BRIGHT FLASHES

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The latency in man between a flash of light in the eyes and the electrical response in the occipital sensory cortex has been said to lie between 25 and more than 100 msec. Some uncertainty also exists about the polarity of the first occipital potential after the flash. Probably a large part of this uncertainty is due to the fact that the earliest parts of the responses are very small; this makes them difficult to identify amongst the relatively large spontaneous activity in the electroencephalogram (e.e.g.). Cobb & Morton (1952), using a superimposition technique (Dawson, 1947) found a clear surface positive wave with a latency of about 70 msec; this was preceded by much smaller deflexions which began perhaps as little as 22 msec after the flash. They were unable to decide whether these small early waves were of cortical origin, or whether they were produced by passive spread of current from the electroretinogram (e.r.g.). Since they coincided approximately with the 'b' wave of the e.r.g. this last possibility seemed quite likely. More recently Calvet, Cathala, Hirsch & Scherrer (1956), using a photographic averaging method, found a positive potential in the occipital region with a latency of 30–40 msec. Monnier (1957) has made measurements from records of 5 responses superimposed and gives the figure of 37.5 msec as the time from the flash to the first, positive-going, occipital potential in healthy subjects. Ciganek (1958), also using a superimposition technique, reports responses with an initial phase in which the occipital region becomes negative 25–35 msec after the flash. It is the purpose of this paper to present evidence, which has been obtained by more sensitive methods of recording, about the latency and form of the occipital potentials evoked by flash stimuli. This evidence, which has been reported in abstract elsewhere (Cobb & Dawson, 1956) supports the view that the early waves described by Cobb & Morton (1952) are of cortical origin and that the initial wave, when it can be recorded, is positive-going in the occipital region and has a latency of 20–25 msec.

METHODS

Eleven healthy adult subjects were used. They were examined lying face downwards with the head and thorax supported on soft pads, to secure the best relaxation of the neck muscles. In front of the face was an opal glass screen subtending an angle of 48° at the eyes. The surface of the screen contained no detail except when the effects of fixation were being studied. Then, a weak red light about 3 mm in diameter was placed in the middle of the screen. The back of the screen was illuminated by the discharge of a capacitor through a Xenon-filled flash tube and the front by the low level of ambient illumination in the darkened laboratory. The capacitor was charged to 2 kV and was usually of 16 μF , giving an energy in the flash of 32 J, but to alter the apparent brightness of the flash it was varied between 0.2 and 16 μF (0.4–32 J), the voltage being kept constant. With the 16 μF capacitor the peak luminance of the flash at the front of the opal screen, measured as described by Cobb & Morton (1952), was around $3.4 \times 10^6 \text{ cd/m}^2$ (10^6 ft-lamberts). The flash had a rapid rise and an approximately exponential decay with a time constant of 90 μsec , giving an integrated luminance with respect to time of $3 \times 10^3 \text{ cd/m}^2 \cdot \text{sec}$. To reduce possible interaction between the responses to one flash and the later parts of the response to the flash preceding it, the rate of flashing was usually kept at one in 2 sec or slower. The occipital potentials were picked up with 1 cm diameter brine-soaked pads or with hypodermic needles blunted and spring-loaded on to the scalp (Dawson, 1954*b*). One electrode was placed on the external occipital protuberance (EOP) on the mid line; others at 3 cm intervals in front of it and also on lines 3 and 6 cm lateral to the mid line. An extra electrode was sometimes used 3 cm below the protuberance on the neck muscles in the mid line. Records were made from one or two pairs of these electrodes and the responses to between 55 and 220 flashes were averaged instrumentally (Dawson, 1953, 1954*a*). The polarity of connexion was such that when the electrode indicated in the figures by a continuous line became negative with respect to the electrode indicated by a broken line, an upward deflexion resulted in the record. The resistance-capacity coupled amplifiers used to feed the averaging machine had enough amplification to give a deflexion on the display cathode ray tube of 2 cm for an input of 2 μV . The high-frequency response of the recording system was limited by the sampling rate of the averaging device; each sample representing the mean potential over a period of 1.6 msec. For reasons dealt with elsewhere (Dawson, 1954*a*) the low-frequency response of the amplifiers was reduced as far as possible without gross distortion of the evoked potentials. The degree of distortion permitted is indicated by the calibration traces in Figs. 1 and 2 and corresponds to a coupling time constant of approximately 0.05 sec. The reduction of low-frequency response was carried out in one coupling only, to minimize phase shift. The other couplings in the amplifier had time constants of not less than 0.5 sec. The e.r.g. was recorded between a contact shell, with an electrode moulded into it, on the cornea and a pad on the forehead.

RESULTS

Relation of occipital responses to e.r.g.

When a subject is stimulated with flashes of the brightness used in these experiments and in the earlier ones of Cobb & Morton (1952, 1953) the e.r.g. recorded between cornea and forehead has an amplitude of about 200 μV . The initial phase of the occipital potentials recorded after the same flashes is rarely as big as 5 μV , and is usually much less. The recording methods used give great sensitivity but they can only discriminate against potentials which are not systematically related to the stimulus.

The possibility therefore exists that the small potentials picked up in the occipital region early after the flash are not part of the e.r.g., but are due to spread of current from the much larger e.r.g. That this is unlikely is shown when the e.r.g. and the occipital potentials are recorded simultaneously as in the records in Fig. 1*a*. Here 110 traces of the e.r.g. have been superimposed, trace 2, and the 110 occipital potential responses to the same stimuli have been averaged and recorded on the same time scale,

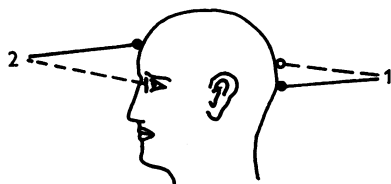
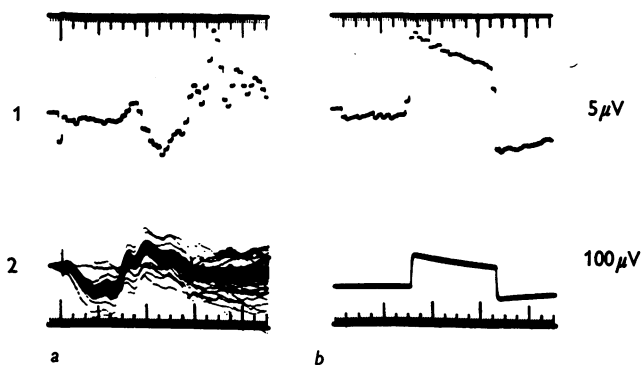


Fig. 1. The record in trace 1*a* is the average of the occipital potentials evoked by 110 bright flashes. In trace 2*a* are shown, superimposed, the retinal potentials produced by the same 110 flashes. In spite of the very high amplification used for trace 1 (voltage calibrations for the two traces are shown in *b*) there is no evidence of electrical spread to the occipital record of the retinal potentials. In these and all later records an upward deflexion indicates that the electrode shown connected by the broken line became positive with respect to that connected by the continuous line. The time scale shows intervals of 1, 5 and 20 msec and the time of occurrence of the stimulus is shown by the first large spike.

trace 1. The 'a' wave of the e.r.g. begins within 5 msec of the stimulus, reaches a maximum 13 msec after the stimulus and remains at about this level for 10 msec. During this time no significant deflexion appears in the occipital record. At 20–25 msec after the flash a series of considerable deflexions begins in the occipital record; none of these is synchronous with any potential having the same time course in the e.r.g. It therefore seems likely that spread of current from the e.r.g. plays no significant part in producing the occipital potential changes. Artifacts due to the heavy pulse of current through the lamp sometimes occur (Fig. 3*b*), but they

have not been found to last more than 1 or 2 msec after the flash was triggered. In the same way any photo-electric effects which occur disturb only the start of the trace and can be controlled by shading the electrode affected. Other sources of potential change systematically related to flashes which need to be considered are the ear and the auditory cortex. The records in Fig. 3*b* suggest that the clicks produced by the lamp are unimportant. In these records 110 sweeps were averaged while the lamp, although flashing and clicking, was covered up so that no light reached the subject. No detectable response occurs after the stimulus marker. However, when the experiment was repeated with the lamp uncovered the responses shown in Fig. 3*a* were recorded. It may fairly be concluded therefore that the initial phase of the occipital potential change represents events in the occipital cortex at about the time of arrival of the group of afferent impulses or shortly after this.

Latency of e.e.g. responses

The initial deflexion in the e.e.g. in Fig. 1 has an average amplitude of 1-1.5 μ V. Although it was sometimes smaller than this, it was clear enough in nine of the eleven subjects for its start to be timed; in all these cases it lay between 20 and 25 msec after the flash. Superimposed on the rather variable slow waves which succeed the first e.e.g. deflexion is a series of faster waves. In nine subjects it was possible to measure from 4 to 7 of these waves and their period was found to be between 8 and 11 msec. In the responses recorded in Fig. 1 the mean period of the 5 waves is 10 msec, which corresponds closely with the period of the fast waves in the e.r.g. (Cobb & Morton, 1953). This may suggest that the fast waves in the e.r.g. represent the synchronized volleys of impulses which are known to leave the retina in some circumstances (Granit & Therman, 1935). Even if this is so, these waves are of little value in establishing the time of conduction from retina to cortex, because of the difficulty of identifying the corresponding waves of each series.

Location and polarity of e.e.g. responses

To avoid picking up the potentials from the eye, or from other parts of the brain, the occipital responses have usually been recorded from pairs of electrodes closely spaced in the occipital regions. Since either or both of such a pair of closely spaced electrodes may be affected by the change of potential during the response, no decision can be arrived at about the polarity of the evoked potentials until their source has been located. Attempts were therefore made to define the potential gradients in the occipital region during the responses, but this was found to be difficult, particularly in the anteroposterior direction. Reversal of the sign of the

gradients, indicating a maximum of activity, could usually be found when the electrodes had a separation of 6 cm, but attempts to define the point of reversal more accurately, by using electrodes at 3 cm intervals, sometimes led to the potential differences picked up during the initial phases of the responses being too small to detect, even when several hundred responses were averaged. In Fig. 2*a* records are shown from a subject in whom the potential gradients, though small, were well defined. Each trace in this figure represents the average of 220 single responses, and since only two averaging channels were available, the records were made in

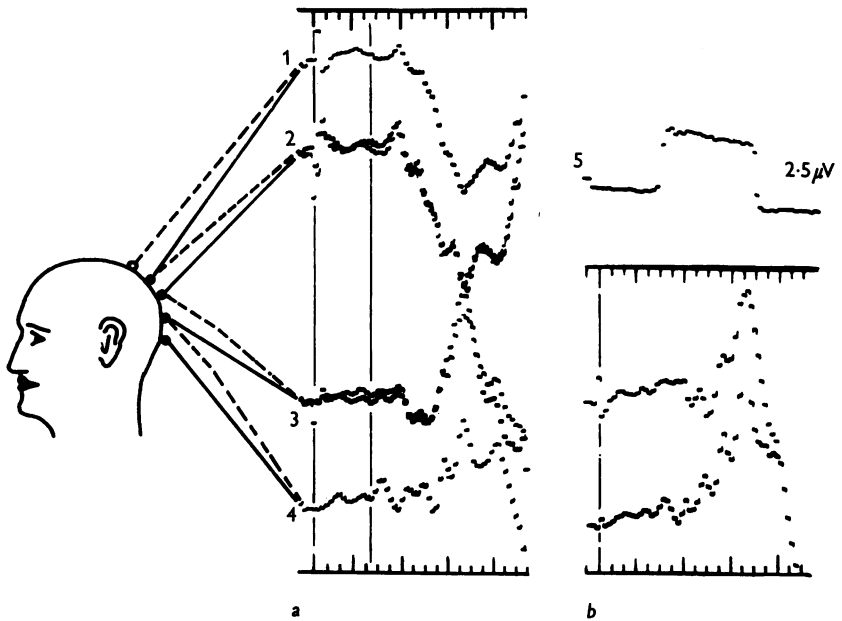


Fig. 2. The records in *a* show the potential gradients along the mid line in the occipital region and are the average of the responses to 220 flashes. The records were made in pairs, 1-2, 2-3 and 3-4. The duplicate records in traces 2 and 3 have been superimposed photographically and were made at intervals of 11 and 22 min. The records in *b* were made from similar electrode positions to those in traces 3 and 4 but more than 3 months later. The first vertical line shows the time of the stimulus and the second the start of the response. The time scale shows intervals of 5 and 20 msec. Trace 5 in *b* shows the voltage calibration for all channels.

pairs, 1-2, 2-3 and 3-4. The duplicate records in channels 2 and 3 have been superimposed photographically. The initial wave of the e.e.g. response is largest in trace 4, where it appears as an upward deflexion starting at 20-22 msec. It is absent in trace 3 and in traces 1 and 2 it appears as a small downward deflexion. This shows that during the first wave a region centred somewhere between the electrodes 3 and 6 cm from the EOP became positive with respect to other parts. From subject to subject this

location has varied slightly between the EOP and a point 6 cm in front of it, on the mid line. In records taken between an electrode on the mid line, 3 cm above the EOP, and others lateral to it, the later, larger waves in the responses appear symmetrical. The initial wave also sometimes appears symmetrical about the mid line; an example of this is shown in Fig. 3*c*, but more often when the central electrode is placed as near the mid line as can be measured from external landmarks, the first wave appears asymmetrical, as in the records in Fig. 3*a*. When the first wave is symmetrical in the records the sense of the deflexions in the traces shows that the mid-line electrode has become positive with respect to the lateral ones.

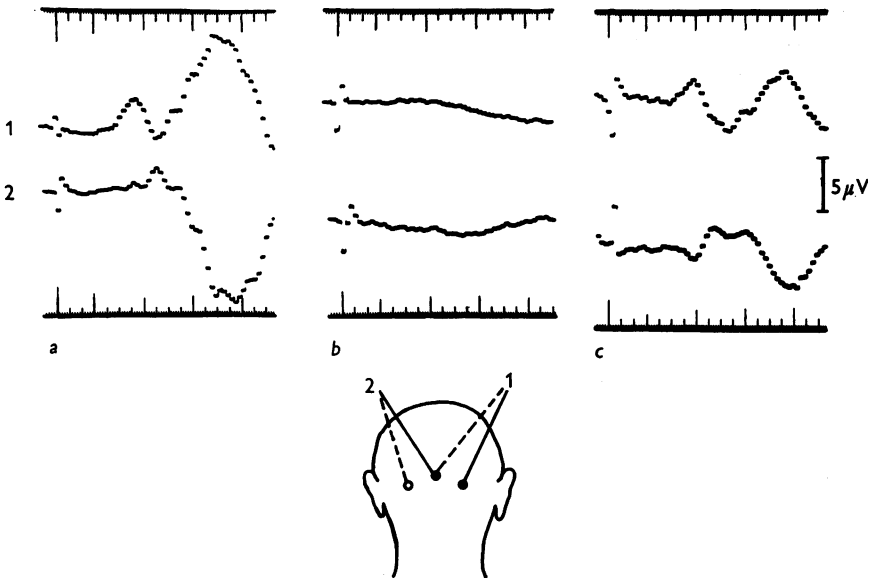


Fig. 3. Record *a* shows the average of the responses to 110 flashes with the recording electrodes across the mid line. In *b* the conditions were the same except that the lamp was covered up, showing that neither the click nor the electrical field produced by the discharge through the lamp causes any significant artifact at the time of the occipital response. The records in *c*, from another subject, where the initial wave is more symmetrical about the mid line, show that in the first wave of the response the electrode on the mid line becomes positive with respect to those lateral to it. The time scales show intervals of 1, 5 and 20 msec.

After the initial positive deflexion in the e.e.g. a series of other waves follows. From the records in Fig. 2 it can be seen that the relative sizes and forms of these later waves is greatly affected by small movements in position of the recording electrodes. However, of these waves the first three appear to have a high degree of constancy. Immediately after the initial positive deflexion is a negative-going potential with its trough at 35–45 msec. Succeeding this there occurs a large positive potential with

its peak at 60–70 msec which sometimes appears to have a potential distribution rather different from that of the initial positive wave. In the records in Fig. 2 the potential gradient over the occipital region during the second large positive wave reverses in sign at a point 6 cm in front of the EOP, whereas these records suggest that the potential gradients during the initial positive deflexion reverse in sign 1 or 2 cm more posteriorly than this. After this large positive deflexion there occurs a relatively much larger negative potential of the order of 5–10 μV in size. This late negative wave has its peak at round about 90–100 msec and it may be this which can sometimes be seen preceding the occiput-positive wave that appears in ordinary e.e.g. records taken during flash stimulation. All the records which are reproduced in this paper showed these four major components, the initial positive wave, the negative wave following it, the second positive wave and the later large negative wave. In two of the subjects, however, those from whom the records shown in Figs. 1, 2 and 4 were taken, the second positive wave is to some extent obscured by the fast ripple which appears with high flash intensities. The other two subjects, those giving the records shown in Fig. 3*a, c*, do not show these fast waves and the peak of the second positive wave is clearer. The recording methods available were not convenient for studying the later parts of the responses succeeding the first 100 msec.

Constancy of the responses

Under fixed conditions of stimulation, observation of single responses suggests that they vary in size considerably from one stimulus to the next. A great part of this apparent variability may be due solely to the background of spontaneous e.e.g. activity on which the evoked potentials are superimposed. In the averaged records, however, the main characteristics of the responses in one person remain little changed over periods of 20 min or more. This is shown in Fig. 2*a*, where the superimposed records of trace 2 were taken at an interval of 11 min and the pair in trace 3 at an interval of 22 min. The records taken at these intervals agree well and they give an indication of the degree of confidence which can be placed in the averaged responses obtained in this type of experiment. Over longer periods, such as that at which the records in Fig. 2*b* were taken, rather more than 3 months after those in Fig. 2*a*, it can be seen that, although the general character of the responses is unchanged, small variations in the relative sizes of the different phases occur. This order of variation in the form of the responses may easily have been caused largely by slight differences in electrode position between the two examinations.

Another factor altering both the relative sizes and latencies of the components of the responses is the brightness of the flash used. When

the flash strength is reduced, by reducing the size of capacitor which is discharged through the lamp, two effects occur. The latency of the initial waves of the response is increased and the amplitudes of all the waves in the response are reduced. In the record in Fig. 4*a* a capacitor of $16 \mu\text{F}$ ($32J$) was used and the initial positive deflexion in the e.e.g. response to the flash has a latency of 20–25 msec to its start. As the flash strength is reduced, little alteration appears down to a capacitor of $4 \mu\text{F}$ ($8J$; Fig. 4*b*) except that the size of the ripple of fast waves with a period

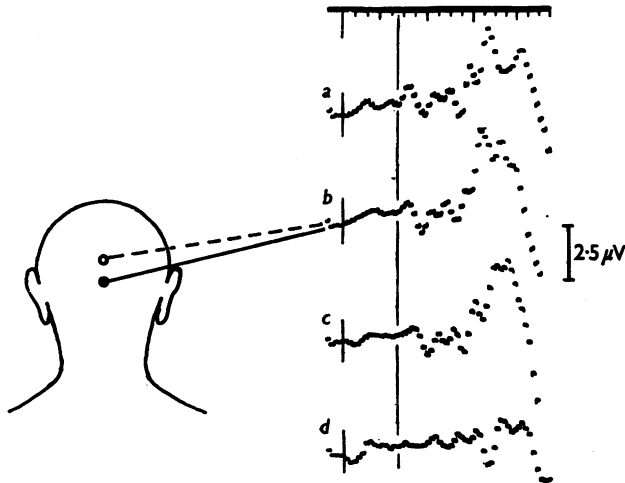


Fig. 4. The records show the effect on the occipital responses of reducing the apparent brightness of the flashes by reducing size of the capacitor discharged through the lamp. In *a* the capacitor was $16 \mu\text{F}$, giving an energy in the flash of $32J$; in *b*, $4 \mu\text{F}$ ($8J$); in *c*, $1 \mu\text{F}$ ($2J$) and in *d*, $0.2 \mu\text{F}$ ($0.4J$). The time of the stimulus is indicated by the first large spike in the time scale and the vertical lines through each record, and the start of the response in record *a* by the second vertical line. As the flash strength is reduced the latency increases and the amplitude of all parts of the response falls. The time scale shows 5 and 20 msec intervals. Average of 220 responses.

of 9–10 msec is reduced. A further reduction of the capacitor to $1 \mu\text{F}$ ($2J$; Fig. 4*c*) causes a distinct reduction in the size of the initial positive wave and an increase in the latency of its start to 25 msec. When the capacitor is reduced to $0.2 \mu\text{F}$ ($0.4J$; Fig. 4*d*) the flash appears to the subject to be much less bright and the latency of the initial positive wave increases to 30 or 35 msec; at the same time its amplitude is approximately half what it was in the top record, *a*, for which the $16 \mu\text{F}$ capacitor was used. No records are available to show how much of this increase in latency with a weaker flash is due to an increase in the retinal delay.

During some experiments it seemed that as the subject's attention was attracted to the auditory field, e.g. by conversation in the room, a change in

size of some of the responses occurred. Unfortunately this effect could not be maintained constant for a sufficiently long time for it to be recorded, but it was found that a change in the form and size of the response of the same type could be produced by visual fixation. The records in Fig. 5 give an example of this type of alteration. The upper record, *a*, shows the average response recorded when 110 flashes were delivered with the subject looking at the opal glass in front of the flash tube without any detail in the field and at a low level of steady illumination. In the lower record in Fig. 5*b* the conditions were the same except that the subject, throughout the time during which the flashes were being delivered, fixed his attention on a small red light in the middle of the opal glass. During this period of fixation the negative-going second wave, with its trough at 45 msec, was

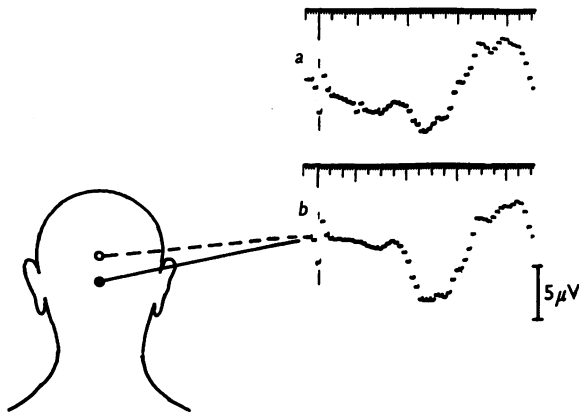


Fig. 5. The records show the average of the responses to 110 flashes. In *a* the opal screen in front of the lamp was blank. In *b* the subject fixed his gaze on a small red light in the middle of the screen throughout the period of stimulation. While the subject was looking at the red light the second, negative-going, wave of the occipital response was increased in amplitude. The time scale shows intervals of 1, 5 and 20 msec.

considerably increased in size. A difference of this sort between any two successive single responses is probably within the range of spontaneous variation, but since each record in the figure was the average of 110 responses, we believe the difference to be significant. At the same time as the negative wave increases in size, the duration of the initial positive wave is reduced, as though cut short by the development of the negative wave.

DISCUSSION

The results presented in this paper appear to resolve the doubts remaining from the previous work of Cobb & Morton (1952) about the latency of the occipital responses to flash stimuli. The records obtained

with averaging methods show clearly that a positive potential appears in the occipital region 20–25 msec after a bright flash stimulus. Comparison with a simultaneous record of the e.r.g. suggests strongly that the small positive potential in the occipital region is not due to a spread of potential from the eye. Other sources of artifact, such as electrical or photo-electric interference from the lamp, or potential changes from the auditory cortex caused by the noise of the discharge in the lamp, have also been excluded. It seems likely therefore that this initial positive wave in the occiput is analogous to the positive wave which may be found on the scalp over the somatic sensory receiving area after a peripheral stimulus and which has been taken to indicate the arrival of the afferent volley at the cortex. However, it must be noted that the positive potential evoked by somatic sensory stimulation may be preceded by a variable negative potential, usually less than $1 \mu\text{V}$ in size. The size of this negative wave varies both with the electrode position (Dawson, 1954*a*, Fig. 6) and with the particular peripheral nerve stimulated (Dawson, 1953, Fig. 12). No such initial negative potential has been recorded in these studies; probably if it occurs it is too small for the present recording methods to reveal it. Also in these experiments no sign has been seen of the brief initial spikes described by Marshall, Talbot & Ades (1943) when recording from exposed cat cortex and stimulating the optic nerve. The failure to record these spikes may be due either to the fact that they are much smaller when the stimulus is a flash to the eye rather than a shock to the optic nerve, as was shown by Marshall *et al.* (1943) or to the limited resolution of the recording method, both in time and in space because of the presence of the skull and scalp.

If it is accepted that these small potentials which we have recorded from over the occiput are in fact an indication of the arrival at cortex of the group of sensory impulses produced by the flash stimulus, or of the events shortly after this, then two chief points must be considered. In the first place Ciganek (1958, 1959) has stated that during the first wave of the evoked potential the occiput becomes negative with respect to other parts of the scalp, whereas we have found that during the first part of the response the occiput becomes positive. Secondly, Monnier (1957) gives the figure of 37.5 msec and Gastaut (1949) the figures of 40–45 msec for the latency between the stimulus and the start of the first wave of the response, whereas we have found a latency of 20–25 msec to the first wave. Both these differences probably arise from the very small size of the initial wave of the evoked potential. Cobb & Morton (1952) found that they could not be certain whether the first wave was present, even when large numbers of records were superimposed and the greatest possible care was taken to obtain muscular relaxation and to avoid other

artifacts which might confuse the record. With the averaging method, on the other hand, the occiput-positive first wave has been a constant feature of the responses, except when the recording electrodes have been symmetrically placed with respect to the peak of the potential gradients, as in trace 3 of Fig. 2*a*. It seems likely therefore that the deflexions taken as the first waves of the responses by Ciganek, Monnier and Gastaut were in fact the second or later waves. In several of the records shown by Ciganek (1959), notably Figs. 1 and 3 of that paper, there is a strong suggestion of a positive-going deflexion (downward in his display) preceding the negative deflexion which he takes as the first wave of the response. The start of this downward deflexion in his Fig. 1 appears to be at about 20 msec after the stimulus and its peak at about 25 msec; this would agree well with the start and the peak of the first positive wave that we record with the averaging technique. Probably therefore no conflict arises between our results and those of Ciganek. Brazier (1958), who used a cross-correlation technique, was also able to detect small occipital potentials starting some 20 msec after a flash stimulus.

The rather greater discrepancy between our results and those of Monnier (1957) and Gastaut (1949) may in part be due to a factor additional to the very small size of the initial positive potential. With the very bright flashes we have used the latency of the e.r.g. was 3–5 msec. It is difficult to compare this with the results of Monnier and Gastaut as they give no figure for the start of the e.r.g.; they do, however, give 30 and 40 msec for the start of the 'b' wave in their records. The start of the 'b' wave in our experiments is probably represented by the inflexion in the downgoing slope of the 'a' wave of the e.r.g. in Fig. 1. This occurs 10 msec after the stimulus. It seems therefore that the latency of the e.r.g. in our experiments may have been 10 or 20 msec less than in those of Monnier and Gastaut. How far such a reduction in latency of the e.r.g. is accompanied by corresponding reduction of the latency of the discharge in the optic nerve is not clear, but the over-all latency of the occipital responses in our experiments may have been not just *apparently* shorter, because of their small size, but really shorter than in the experiments of Monnier and Gastaut. Here again then it seems that there may be no real discrepancy between our results and those of Monnier and Gastaut. The differences merely emphasize the need for a complete specification of the conditions under which experiments of this kind are carried out.

Another factor in the stimulus situation which needs as full a description as possible is the amount of detail in the visual field and the degree of attention being paid to it. From the records shown in Fig. 5 it seems that concentration on a small red light in a previously blank field can cause an increase in size of the negative second potential in the response which

might be sufficient to raise the wave above the lower limit of detectability in superimposed records. It is not clear whether this increase in size of part of the response which accompanies a concentration of attention on the visual field represents an inverse effect to that described by Hernández-Péon, Guzmán-Flores, Alcaraz & Fernández-Guardiola (1957). They found that the occipital responses to flash stimuli in an anaesthetized cat were reduced when the animal's attention was attracted to another sensory field and they were able to show that there was a reduction in the size of the afferent volley at a subcortical level. That this effect, and the opposite effect also, may occur in man has been shown by Jouvet & Courjon (1958), who recorded, from an electrode implanted in the optic radiation, an increase in the size of the afferent volley when the subject concentrated on a visual stimulus. The only evidence available from our records on this point is the fact that when the negative second wave is increased, as in the record in Fig. 5*b*, the initial positive wave is not increased in size and may even be a little reduced. This may be slight evidence that the afferent volley has not increased in size, as the development of a large negative second wave in an evoked potential may cut short the positive initial wave. However, it has generally been the case in experiments on man that an increase in the strength of a somatic stimulus and an increase in the ascending volley in the peripheral nerve, although they sometimes lead to a disproportionate increase in the size of the negative wave of the evoked potential, have not caused this increase without an increase in the positive wave also (G. D. Dawson, unpublished observations). Since the positive wave was not increased, it may be suggested that this effect is more like those described by Dumont & Dell (1958) and Bremer & Stoupe (1959). They found that the size of the cortical response to stimulation of the optic nerve could be increased by stimulation elsewhere, and they showed that this effect was due more to a change in the state of the responding cortex than to an increase in the afferent transmission. An increase of the negative second wave of the somatic evoked potential without any increase of the positive first wave, or of the volley in the second sensory neurones in the afferent pathway, and thought to be largely intracortical, has also been described by Dawson, Podachin & Schatz (1959), but in these experiments the animals were anaesthetized and the effects of the anaesthetic have not yet been defined.

SUMMARY

1. The occipital evoked potential responses to bright flashes of light have been recorded by an integrating method which allows potential differences less than 1 μ V to be detected.

2. Occipital potential changes of the order of 1–1.5 μV begin 20–25 msec after the flash. Comparison with the e.r.g. recorded simultaneously suggests that these occipital potentials are not due to current spread from the e.r.g. or other artifact.

3. From measurements of the latency of the occipital responses and the e.r.g. it is concluded that the transmission time from the retina to the cortex does not exceed 15 msec, though it could be less than this.

4. The potential gradients in the occipital region show that the initial wave in the e.e.g. is positive-going with respect to other parts of the scalp and has a maximum on the mid line, between 3 and 6 cm above the external occipital protuberance.

5. After the initial positive deflexion there occur a negative-going potential with its peak at 40–50 msec, a larger positive potential with its peak at 55–65 msec and a relatively large (5–10 μV) negative potential with its peak at 90–100 msec. This is followed by a series of waves with a period of about 100 msec.

6. With constant conditions the repeatability of the form of the responses is high over periods of 20 min. Over periods of months the repeatability is also good, though variations in the relative sizes of some of the components appear.

7. Reduction of the apparent brightness of the flash stimulus leads to a reduction in the size of the occipital responses and an increase in their latency.

8. Fixation on a detail of the visual field between flashes may lead to an increase in the second, negative, component of the response and a shortening of the initial positive deflexion.

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