

BRAIN.

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THE BERGER RHYTHM: POTENTIAL CHANGES FROM THE OCCIPITAL LOBES IN MAN.

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INTRODUCTION.

DURING the past five years Hans Berger (1929-1933) has published a series of papers dealing with a remarkable electric effect which can be detected in the human subject by electrodes applied to the head. It consists of a rhythmic oscillation of potential with a frequency in the neighbourhood of 10 a second, appearing when the subject lies quietly with eyes closed and disappearing if the attention is fully occupied. Berger records it by pad electrodes on the scalp or, preferably, by needles reaching the periosteum of the skull. He finds that the waves

are larger when the needles are over an opening in the skull than when they are over the intact bone. From this and other evidence he concludes that the potential changes are produced by the cerebral cortex and that they represent a fundamental activity of the brain.

During the same period a number of workers have recorded the potential changes which take place in the exposed cortex of animals. Their findings have been difficult to reconcile with Berger's as the potential changes have been much less regular and have rarely shown any sign of a persistent rhythm at 10 a second. Our own work on animals (Adrian and Matthews, 1934) led in the same direction. We found it difficult to accept the view that such uniform activity could occur throughout the brain in a conscious subject, and as this seemed to us to be Berger's conclusion we decided to repeat his experiments. The result has been to satisfy us, after an initial period of hesitation, that potential waves which he describes do arise in the cortex, and to show that they can be explained in a way which does not conflict with the results from animals.

The present paper is chiefly concerned with the nature of the potential waves, the structures responsible for them and the kind of activity which they represent. To anticipate it may be said that we regard the effect as due to a spontaneous rhythmic activity of a group of cortical cells in some part of the occipital lobe. These tend to beat synchronously when they are undisturbed, but visual activity or widespread non-visual activity in the brain breaks up the rhythm by exposing the cells to a mosaic of excitations which makes synchronous action impossible. Berger, if we have interpreted him correctly, regards the waves as having a much wider and less specific origin, but the evidence as to localization is the only important point on which our results seem to differ from his.

Since the effect is so characteristic we shall refer to it in future as the Berger rhythm. Berger calls it the *electrencephalogram*, but the shorter title avoids the suggestion that the rhythm is produced by the entire cortex.

TECHNIQUE.

As the potential waves are of the order of $\frac{1}{10}$ mv. or less they are most conveniently recorded by a valve amplifier leading to some form of oscillograph. To record their exact form and to detect very rapid oscillations as well (e.g. those from muscle) we have used the Matthews oscillograph with a period of $\frac{1}{1000}$ a second recording optically on bromide paper. In the majority of experiments, however, a very high period in the recording instrument is unnecessary and we have found it more convenient to use the Matthews ink-

writer oscillograph which has a period of $\frac{1}{10}$ second. For this we have generally used a balanced input amplifier (Matthews, 1934) followed by two condenser coupled valves leading through a tapped volume control to the second of the three valves of the oscillograph amplifier. The condenser coupling was usually arranged so that slow potential changes would not appear in the record, but controls have been made with amplifiers capable of handling very slow changes without distortion. It is sometimes an advantage to be able to hear as well as see the rhythm; although its frequency is only 10 a second it can be made audible by using a horn loud speaker with the diaphragm set very close to the pole pieces and a condenser in parallel to cut out high frequencies.

As electrodes we have used squares of copper gauze covered with lint and soaked in warm saline. These are fixed in position by a head bandage, the hair under them being parted so as to ensure that they make good contact with the scalp. Since the amplifier takes no appreciable current from the electrodes the precise value of the skin resistance does not affect the size of the potential waves. In a few preliminary experiments we followed Berger's technique, using steel needles thrust through the scalp, but we were relieved to find that pad electrodes gave equally good results. Berger stresses the importance of absolute quiet and keeps the subject on a couch in a room separate from the recording system. In the laboratory, with research workers as subjects, good rhythms can usually be obtained with the subject sitting in a chair, though complete relaxation of the neck muscles has the advantage of giving a smoother base line. In certain experiments (e.g. with blind patients) the room was kept as quiet as possible and the subject lay on a bed.

THE ORIGIN OF THE RHYTHMIC POTENTIAL WAVES.

Fig. 1 gives typical records of the Berger rhythm made with pad electrodes on the vertex and occiput and fig. 2 shows the essential condition for its appearance, namely that there should be an absence of visual activity¹: thus in fig. 2, A and B it develops on closing the eyes, in fig. 2, C it disappears when they are opened in a lighted room and in fig. 2, D it is present when they are open in the dark. There is often more variation in the size of the waves and sometimes the rhythm only appears intermittently, but its frequency is so characteristic and so constant that there is never any doubt as to its presence. With pad electrodes the potentials are at a maximum of about $\frac{1}{10}$ mv. when one of the pads is just above the external occipital protuberance and the other is 3 in. or more away. What evidence is there to show that these potentials are developed in the brain?

Berger has discussed the evidence very fully and has carried out

¹ More correctly, an absence of the activities connected with pattern vision (see p. 367, paragraph 2).

numerous controls. The most direct proof of a cerebral origin is his finding that with needle electrodes the potentials are largest when the needles pierce the scalp over an opening in the skull. This is perhaps

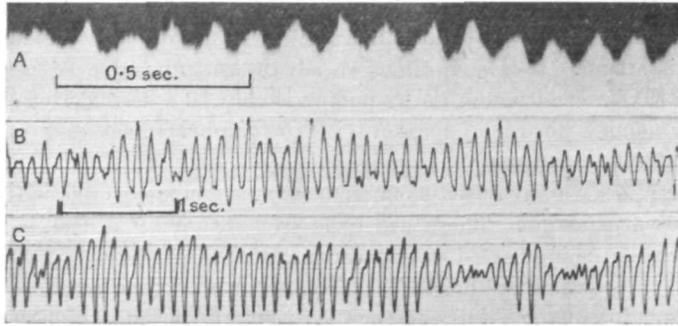


FIG. 1.—Records of the Berger rhythm made with pad electrodes on the head (vertex and occiput), the subjects sitting with eyes closed.

- A. Subject E. D. A. Record made with Matthews' oscillograph, period $\frac{1}{10}$ sec. Maximum excursion 0.07 mv. Frequency 9.5 per sec.
 B. Subject W. H. Record made with ink-writer oscillograph, period $\frac{1}{10}$ sec. Frequency of waves 9 per sec.
 C. Subject K. Y. Record made as in B. Frequency 10.5 per sec.

N.B.—All ink-writer records are at the same speed. Of the subjects examined by us, W. H. gives the slowest and K. Y. the most rapid rhythm.

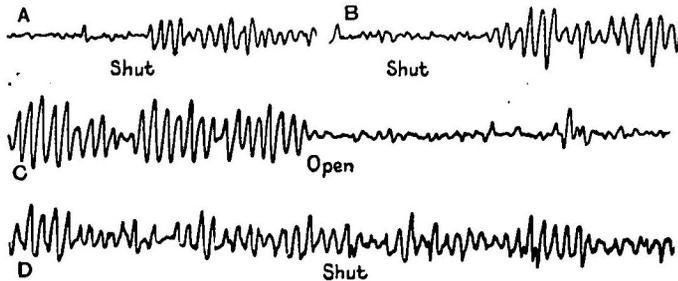


FIG. 2.—The development of the rhythm in the absence of visual activity.

- A. E. D. A. The rhythm appears when the eyes are closed.
 B. B. H. C. M. Ditto.
 C. E. D. A. The rhythm disappears when the eyes are opened.
 D. W. H. After some minutes in the dark the rhythm is present with the eyes open. Closing them does not alter the rhythm.

enough in itself, but we were unconvinced until we had satisfied ourselves (*a*) that the waves are not due to the eye muscles or to movements of the eyeballs and (*b*) that there is no need to postulate an origin from the whole surface of the brain, but only the occipital lobe. The discussion of these two points will show the general nature of the problem and of the evidence at our disposal.

Evidence against an orbital origin.—The chief source of uncertainty can be seen from the diagram in fig. 3. The skull forms a box with walls of relatively high resistance and the scalp is a thin sheet of conducting material leading to the various muscles of the face and neck. Thus a contraction of almost any of them can give rise to potential oscillations between electrodes on the scalp and a muscle like the temporal or occipito-frontalis can give oscillations much larger than the waves of the Berger rhythm. Fortunately the electromyogram of a normal sustained contraction is a rapid irregular affair quite unlike the 10 a second rhythm; but the muscles cannot be ruled out altogether, for waves of the required form and regularity might be produced by a clonus or tremor in which all the motor units contract synchronously.

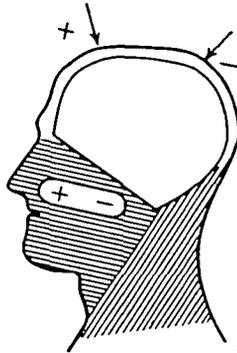


FIG. 3.—Showing how electrodes in the scalp may be affected by action currents in the face and neck owing to the high resistance of skull.

The most likely place for such a clonus is the orbit. The Berger rhythm is obviously connected in some way with the visual mechanism, and in all the conditions in which it appears there is a lack of ocular fixation. It is possible that shutting the eyes or the presentation of a uniform field would allow some of the eye muscles to develop a rhythmic beat. This would disappear as soon as the visual attention was aroused and it would give regular potential waves in the muscles.

For a time we suspected that the rhythm arose in this way, but it was soon clear that the external eye muscles are so deeply buried in the orbit that their action currents can have little effect on electrodes applied to the scalp. We found that active and passive movements of the eyeball were equally ineffective: with the electrodes on occiput and vertex the jerky eye movement produced by looking at the spokes of a revolving wheel gives no corresponding potential waves, and

an oscillation of the eyeball by a clockwork-driven rod has no detectable effect though the eyeball is moved through several degrees.

Again, the rhythm is not dependent on a particular posture of the eyes (for it can occur with the lids open or closed) and is not necessarily interrupted by eye-movements. When the eyes are open in the dark and the rhythm is well developed, a movement of the eyes to left or right or a closure of the lids will cause no break in the sequence of waves (fig. 2, D). Blinking or firm closure of the eyelids may produce large potential changes, for the orbicularis is a surface muscle, but we have failed to produce any evidence of potential changes due to the eyeball or its muscles. And in any case the potential gradients would be at a maximum in the neighbourhood of the eye, whereas the waves of the Berger rhythm are at a maximum over the occipital part of the skull.

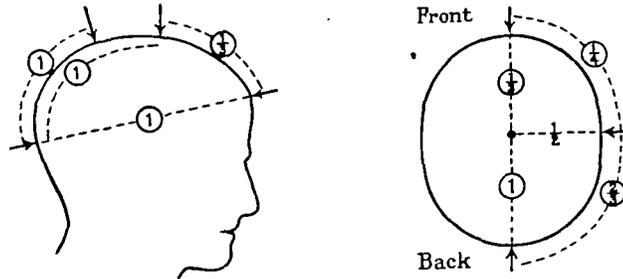


FIG. 4.—Rough estimate of average size of waves with different electrode positions in subject W. H.

Localization of potentials.—The distribution of the potentials over the head is a point of great importance, both for the exclusion of eye movements and for deciding the part of the brain responsible for the rhythm. Berger seems to believe that every part of the cortex may contribute to the potential changes (Berger, 1933A, fig. 3, &c.), and it is true that the waves can be detected in almost any part of the scalp; but in every case examined we have found that to produce the maximum amplitude one of the electrodes must be slightly above the external occipital protuberance. The position of the other is then immaterial provided that it is at least 3 inches away.

Since the waves vary in size from moment to moment it is impossible to make an accurate comparison of different electrode positions, but the diagrams in fig. 4 give a rough estimate of the relative sizes and the records in fig. 5 show the kind of data on which the

diagrams are based. It will be seen that with one lead on the vertex and the other on the forehead the waves are on the average one-half or one-third as large as they are with the leads on vertex and occiput. With both leads near the eyes the rhythm can rarely be detected at all. These facts are definitely opposed to the idea that the rhythm arises from structures in the orbit. They cannot be taken as a conclusive proof of origin from the occipital lobes rather than some other part of the brain, for the distribution of potential gradients outside the skull might depend on the thickness of the bone, the presence of blood sinuses, &c., in different regions. The best proof that the waves do in fact arise in the occipital part of the brain comes from patients

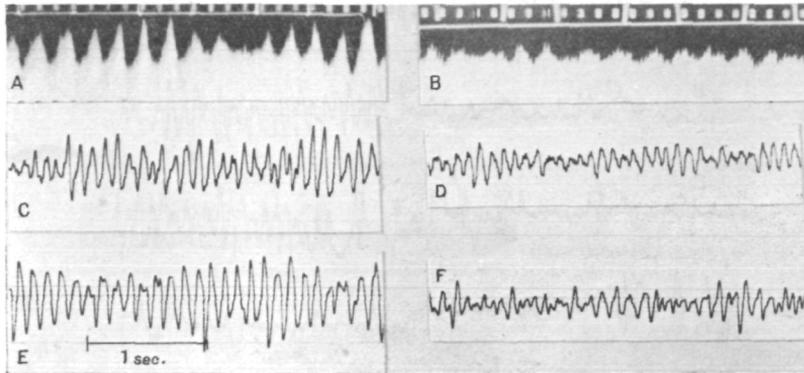


FIG. 5.—Comparison of waves recorded from the back and front of the head in different subjects.

- A. E. D. A. Electrodes on vertex and occiput. B. On vertex and forehead.
- C. C. L. P. Vertex and occiput. D. Vertex and forehead.
- E. W. H. Vertex and occiput. F. Vertex and forehead.

In record B the small, rapid excursions are due to muscle action currents.

with openings in the skull and is dealt with on p. 363, where the distribution of potential is considered in more detail.

Evidence against cranial muscles, &c.—Some time has been spent in discussing eye movements as a possible cause of the rhythm because there is no doubt that the eyes are somehow concerned in it. An oscillation of the eye muscles or eyeballs is therefore the most likely cause apart from the brain. If the eyes are ruled out there is still the possibility of a tremor in the muscles of the neck, face, or scalp, but it would be difficult to explain why the eyes must be inactive and still more to explain our failure to influence the rhythm by changing the posture of the head or contracting facial or neck muscles. The head

may be bent forward or back, but the 10 a second rhythm still appears when the eyes are closed and goes when they are opened to the light. If the neck muscles are contracted the rhythm is superimposed on an electromyogram of the usual type but there is no sign that it is altered in any way. The forehead may be wrinkled or the scalp pulled without affecting it.

Other possibilities, e.g. the pulsation of vessels, activity of pilomotor muscles, tremors of the head, &c., have been examined by Berger and rejected. We have considered the possibility of the waves being due to retinal potentials of some kind, but find that electrodes on the scalp

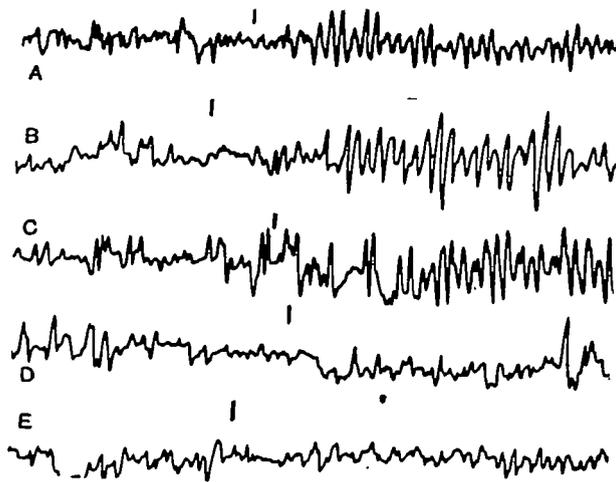


FIG. 6.—Records from patient with bone defect in the right temporal region due to shell wound seventeen years ago. The eyes are closed at the signal.

- A. Electrodes on occiput and left parietal region.
- B. " " occiput and right parietal region.
- C. " " occiput and forehead.
- D. " " forehead and left parietal region.
- E. " " forehead and right parietal region.

cannot even pick up the potential change caused by illuminating the eye suddenly with a bright light.

Evidence in favour of the cortex.—Besides this negative evidence against an extracranial origin there is positive evidence in favour of the brain, derived from subjects with openings in the skull. Berger has examined many of these with needle electrodes in the scalp and finds that the waves are always larger when the needles are over the bone defect, wherever it may be. If the currents arise somewhere inside the skull this result is to be expected, but if they arise outside and are

conducted to the electrodes by the scalp the defect in the skull should produce greater short-circuiting and smaller potential changes.

Our own observations on trephined patients lead to the same conclusion but are chiefly interesting for giving more definite evidence of localization. We have had two patients with small bone defects in the temporal region, one the result of a shell wound and the other an exploratory opening for a condition which developed no further. In both patients the rhythm on closing the eyes was well marked when an occipital electrode was used, but if the electrodes were further forward (e.g. on vertex and forehead) the waves were completely absent (fig. 6). If the skull had been intact they would have been merely reduced in size (cf. fig. 5). Thus the opening in the skull has the effect of confining the potential changes to the back of the head. If the waves have an extracranial origin or an origin from the whole cortex it is hard to conceive any reason for this, but if they come from the occipital part of the cortex the reason is clear enough.

The distribution of current with the skull intact or trephined can be illustrated by rough diagrams, though it must be understood that these can make no claim to take every factor into account. We may start with the assumption that the cortical potentials are due to structures close to the surface of the brain and directed at right angles to it; for the potentials recorded from the exposed cortex are best explained in this way (Adrian and Matthews, 1934). Now, if the skull were a sphere, an area of electrically active cortex would give the distribution of current shown in fig. 7, A, the lines of current flow diverging from a region opposite the active areas.¹ Actually, with the skull intact, the divergence takes place somewhere in the frontal region (fig. 7, B), but there is usually enough difference of potential between vertex and forehead to enable the waves to be recorded there. An opening in the skull will modify the distribution in the way shown in fig. 7, C. The circuit within the brain to the opening and then back in the scalp to the occiput involves only one thickness of bone and so offers a pathway of relatively

¹ Owing to the relatively high resistance of the skull the current will be much more evenly distributed than it would be if the brain, skull and scalp were all the same conductivity. In a homogeneous medium the current flowing along any path would be inversely proportional to the length of the path; thus the lines of current flow would be concentrated in the occipital region. But it will be seen from fig. 7, B that except at the margins of the active region the current must pass twice through the skull to complete the circuit. The soft tissues will contribute a relatively small proportion of the total resistance, and therefore the length of the pathway through them will be relatively unimportant. Thus the longer pathways (through the frontal and parietal bones) will carry an appreciable fraction of the total current.

low resistance from the interior to the active surface: the result is that a negligible proportion of the current will flow through the scalp anterior to the opening.

Three patients with suboccipital decompressions gave evidence of the same kind. In their case the rhythm could not be obtained at all unless one of the electrodes was on the occiput very close to the opening in the bone. As in fig. 7, C, the opening becomes the main pathway from the interior of the brain to the active surface, and, as the active surface is very close to the opening, the potential gradients will be relatively steep in this region but inappreciable over the rest of the skull.

The potential distribution in these cases shows that the active area is somewhere in the occipital region, but the main focus of activity is

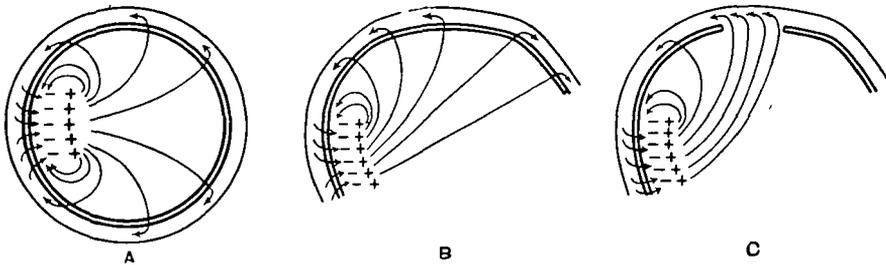


FIG. 7.—Diagrams to show current distribution—A, if the skull were spherical; B, in the median plane with the skull intact; and C, with an opening in the skull.

not at a fixed point in the brain. This can be inferred from records made with two oscillographs leading simultaneously from different regions of the skull. Berger has made many of these and has shown that the relative size of the waves from the different leads is by no means constant. The same result can be seen in fig. 8, A which gives simultaneous records of the potentials between vertex and occiput and vertex and forehead. The relative size of corresponding waves in the two records varies considerably and occasionally the potential change between vertex and forehead is larger than that between vertex and occiput.¹

A result of this kind can only mean that the distribution of current flow in the brain shifts from time to time, but it is not at all incompatible with the view that the activity arises in the occipital region.

¹ The absence of a fixed ratio between corresponding waves from the two pairs of leads accounts for the fact that in records made with the electrodes on occiput and vertex the waves are neither consistently larger or consistently smaller than in records from occiput and forehead (cf. fig. 4). The general direction of current flow in the frontal region varies to some extent with the individual and probably depends on the shape of the head.

A reference to fig. 7, A and B, will show that a movement up or down in the position of maximum activity will produce a corresponding movement in the region at the opposite side of the skull from which the lines of current-flow diverge in the scalp. The direction of movement in the two oscillograph tracings in fig. 8, A shows that the potentials at occiput and forehead rise and fall simultaneously relative to the vertex (in agreement with the distribution given in fig. 7, B) but a shift in the point of current divergence will naturally alter the relative sizes of the waves from the two pairs of leads and may suppress or reverse them in one pair of leads while little alteration occurs in the other.

Further complications probably arise from the beat spreading progressively over the active area, or over some part of it, instead of

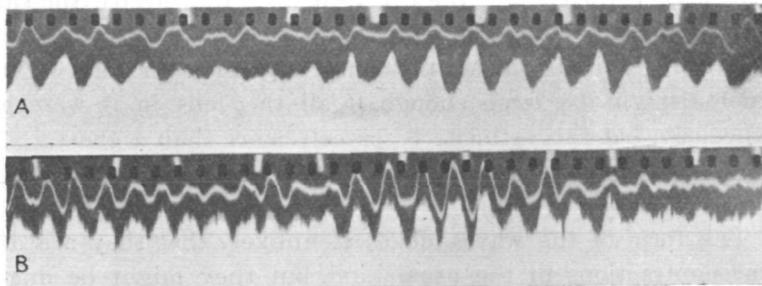


FIG. 8.—Simultaneous records of the waves at two pairs of electrodes.

- A. The white line records the waves between vertex and forehead and the junction between dark and light area records those between vertex and occiput.
 B. The white line records the waves between occiput and right parietal region and the junction between dark and light those between occiput and left parietal region.

appearing simultaneously at every point. In the exposed cortex of animals the large potential changes produced by convulsant drugs are due to waves of activity which travel at a finite rate over the surface (Adrian and Matthews, 1934). Similar waves confined to the occipital region would produce a rhythmic shift in the current distribution corresponding to the rhythmic change in the position of maximum activity, and this might lead to phase differences in the potential waves from different leads.

It will be seen from the diagram that if both pairs of leads are confined to the posterior half of the skull the waves should correspond much more closely. This is found to be so. Fig. 8, B gives simultaneous records, one from electrodes on the occiput and above the right ear and the other from the occiput and above the left ear. The waves

are now almost identical, the potentials at either side rising and falling simultaneously relative to the occiput. This result (from four subjects) makes it unlikely that there is much difference in the phase or extent of the beat in the right and left hemispheres, though occasionally the waves are found to increase in size for a few beats on one side and to decrease correspondingly on the other.

It is to be hoped that a more detailed mapping of the potential distribution over the head from moment to moment will show how far the focus of activity can move. For the present all that can be said is that the active region must cover a fairly large area in the occipital lobe and that it must be close to the surface of the brain. If it were deeply situated the short-circuiting by inactive tissue would be too great to allow the potentials to be recorded through the skull. In general the larger the area involved and the nearer it is to the surface the smaller will be the potential change at each point necessary to set up measurable potential gradients outside the skull. An area one or two inches in diameter might be large enough if all the cells in it were active simultaneously, but this estimate is scarcely more than a guess.

The evidence as to the origin of the potential waves may be summarized as follows :—

(1) The form of the waves makes it unlikely that they are due to muscular contractions of the usual kind, but they might be due to a clonic contraction or tremor.

(2) As the rhythm only appears when there is no ocular fixation, a tremor of the orbital muscles might be responsible.

(3) But rapid to-and-fro movements of the eyes give no corresponding potential waves in the scalp. Also potentials due to the eye muscles would be greatest when one of the electrodes is near the orbit. The waves of the Berger rhythm are greatest when one of the electrodes is near the occiput.

(4) The waves are not due to potential changes in the retina, for these are not large enough to affect electrodes applied to the scalp.

(5) The presence of an opening in the skull modifies the potential distribution in a way which is readily explained if the potentials arise in the brain, but not if they arise outside the skull.

(6) In trephined subjects there is a more definite localization to the occipital region.

(7) The magnitude of the potential waves shows that they are most probably due to the simultaneous or nearly simultaneous activity of a fairly large region on the surface of the occipital lobe.

THE FAILURE OF THE RHYTHM DURING VISUAL ACTIVITY.

The occipital origin of the waves emphasizes their close connection with vision. Berger has shown that the rhythm can be stopped by non-visual activity if the subject's whole attention is involved, but it is stopped far more effectively by a pattern in the visual field, however uninteresting. In fact for the rhythm to appear, either the eyes must be shut, or the central part of the visual field must be uniform and the subject must not examine it too closely.

It is the perception of pattern or the attempt to perceive it that interferes with the rhythm. The perception of light does not affect it: if the eyes are closed the rhythm persists, although the subject is aware that the room is light or dark and can say when the illumination is

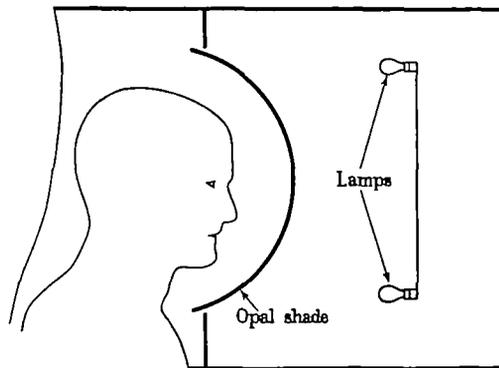


FIG. 9.—Arrangement for giving a uniform visual field with different degrees of illumination.

altered. Again, with the eyes open, the visual field can be made more or less uniform by arranging an opal glass bowl in front of the face and lighting it by a ring of lamps (fig. 9). The rhythm will appear after a time, and when it is established the illumination of the bowl can be varied without causing more than a momentary pause in the waves, provided that the light is not unpleasantly bright. On the other hand, a narrow band of shadow thrown across the field will stop the rhythm at once. Similarly, when the eyes are shut, the circle of light caused by pressure on the eyeball will abolish the rhythm and bright after images will delay its appearance.

Absolute uniformity of the visual field is not essential, however; with the eyes shut the rhythm usually appears a short time before an after image has completely faded, and with the eyes open the peripheral

part of the field may contain some pattern. But sharp contrasts nearer the central part of the field are prohibitive. Thus a few black spots on the opal screen, or a few small holes in the shutters of a dark room, will abolish the rhythm if the subject looks directly at them, but if they come into the peripheral field he may be aware that there is something there and yet the rhythm will persist.

The effect of closing the eyes.—Although there is the same contrast in the effect of a uniform and non-uniform field whether the eyes are closed or open, the closure of the eyes seems in itself to favour the development of the rhythm. The regular waves usually appear half a second or less after the eyes are shut, but if they remain open and the

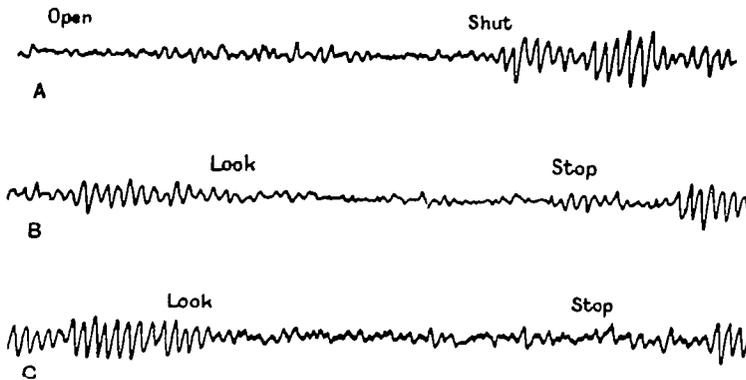


FIG. 10.—Development of the rhythm with the eyes open in the dark. Head enclosed in a box lined with black velvet.

A. During the first few minutes the rhythm only appears when the eyes are closed.
B and C. Later. The rhythm is present with the eyes open but is abolished by trying to see.

field is made uniform the waves may not appear for some minutes. The difference is chiefly noticeable when the subject is first confronted with a uniform field. This may be either the opal screen arrangement or the uniform black field produced by enclosing the head in a box lined with black velvet, or by making the whole room completely dark. To begin with the rhythm will only appear when the eyes are shut (fig. 10, A), and it will cease when they are opened, although the field is uniform. In a few minutes the rhythm will develop with the eyes open. It may still be disturbed when they are opened after a period of closure, but eventually opening them will cease to have any effect.

The most likely explanation is that the act of closing the eyes is coupled with an automatic withdrawal of the attention from visual

phenomena. When our eyes are open we try to see something, even though we are in a room which is too dark for anything to be made out. So with the head before an opal screen or in a dark box the tendency is to look for some trace of detail, and to begin with it is only when the eyes are closed that the subject is completely indifferent to the content of the field. After a time he becomes used to his surroundings and it is easier to open the eyes without expecting and trying to see. It is then that the rhythm persists.

This explanation is based mainly on the introspection of one of us acting as subject. It must be admitted that when the eyes are open in the dark and the rhythm absent the feeling of "trying to see" is often very slight, although at times one may be conscious that one is peering into the blackness. But the explanation is supported by the fact that after the rhythm has become established it can be made to disappear at will by attempting to see some trace of detail in the field (fig. 10, B and C). The attempt is often attended with a feeling of muscular effort which probably implies convergence and accommodation, but the rhythm may go before this is felt.

An effort of the same kind can abolish the rhythm although the eyes are shut. In this case the effort causes a method of convergence which can be felt through the closed lids. But it is perhaps a mistake to group this with the other kinds of visual activity which abolish the rhythm, for it involves considerable mental effort and a non-visual activity of the same kind, e.g. straining the ears to hear a nearly inaudible sound (e.g. a watch ticking), is equally effective. On the other hand, when the eyes are first opened in the dark no conscious straining to see is needed to prevent the appearance of the rhythm.

In the majority of subjects the rhythm becomes more clearly marked after the examination has lasted ten minutes or more. The improvement seems to be due to the repeated periods with the eyes closed. But if they remain closed for a long period the rhythm often becomes more intermittent. It is at its best, with large waves and little fluctuation in size, immediately after the eyes have been opened and closed again—as though the sudden disappearance of the normal visual activity gives the most favourable conditions. This at least is our impression, though the variations from subject to subject and from time to time are too great to allow of any certainty.

Absence of rhythm in blind subjects.—One set of observations supports the impression that the rhythm would not persist indefinitely if the eyes remained closed. We have examined three patients who

have been totally blind for some years and we have been quite unable to detect any sign of the rhythm in them. In one of them (blind for thirty-five years from an accident, with hæmorrhages in the vitreous, &c.) the eye movements were unusually good but closing the lids did not produce the rhythm. Another was a case of double optic atrophy of two to three years' duration, and the third had had both eyeballs removed in 1918 as the result of a shell wound. They were examined lying on a couch in a quiet room, but we could not discover any condition which would cause the rhythm to appear.

The bearing of this result on the cortical mechanism of the rhythm will be discussed later. It is scarcely surprising, for if the most favourable conditions are those which exist just after pattern vision ceases, we might expect that the rhythm would be absent in patients whose pattern vision ceased long ago.

THE EFFECT OF NON-VISUAL ACTIVITY.

In regard to activities other than visual we have little to add to Berger's account. We find, as he has done, that a problem which claims the whole attention will abolish the rhythm though the eyes are shut. A difficult question in mental arithmetic will do so as long as the subject tries hard to solve it (fig. 11, A), but the rhythm will return as soon as his attention wanders. In the same way an attempt to tie or untie as many knots as possible in a given time will abolish the rhythm as long as the subject concentrates his whole energy on the task.

As regards sensory stimulation, the effect seems to depend mainly on the amount of disturbance produced in the subject's mind (or on the amount of "affect"). An unexpected touch by the experimenter in an unexpected region (e.g. the face) will usually stop the waves (fig. 11, B), but the subject can touch his own face or inflict considerable pain on himself without disturbing it. As might be expected, the disturbing effect of questions, commands, &c., is often most pronounced when a subject is examined for the first time: the records in fig. 11 are from subjects who were quite familiar with the procedure.

It will be clear from this that a great deal can go on in the subject's brain and mind without upsetting the rhythm. He can count numbers aloud, repeat familiar poetry or join in an unimportant conversation with, at most, an initial reduction in the size of the wave. The photographs in fig. 5 are an example of the amount of non-visual activity which can go on without interfering with the rhythm, for they were made by one of us working without assistance and recording the waves

from his own head. It is true that no manipulations had to be made after the eyes were closed, but a restful state of mind was scarcely possible. Again some of the evidence on the effect of opening the eyes in the dark was made by one of us listening to the rhythm from his head in a loud speaker. This made it possible to correlate the impression of not looking or looking with the presence or absence of the rhythm. In this case, as when the eyes are opened in daylight, the subject can hear that the rhythm ceases, for opening the eyes does not prevent one from listening; but the non-visual activities which abolish the rhythm demand so much attention that a subject engaged in them

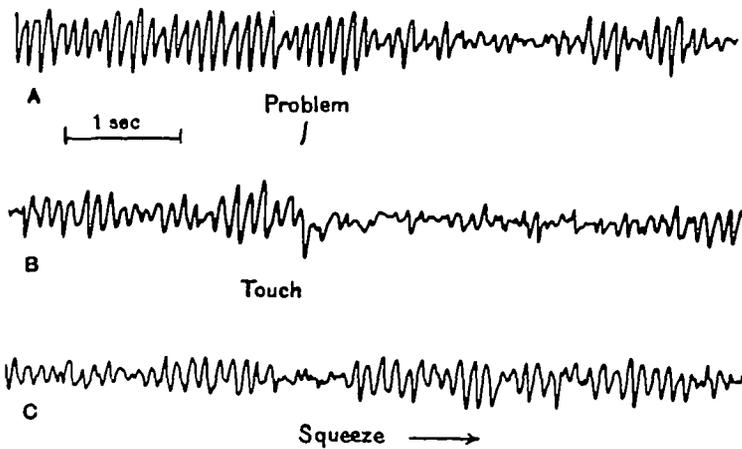


FIG. 11.—A and B. Abolition of the rhythm by non-visual activities.
 A. E. D. A. Eyes closed. Problem in mental arithmetic given at signal.
 B. W. H. Eyes closed. Touch on the nose with cotton-wool.
 C. Persistence of rhythm in spite of muscular effort.
 W. H. Eyes closed, squeezing pliers as tightly as possible.

cannot listen at the same time and can never hear whether the rhythm has been affected or not.

It is interesting to find that powerful muscular contractions do not interfere with the rhythm although the subject exerts his full strength. Thus in fig. 11, c, gripping a pair of pliers as tightly as possible seems, if anything, to reinforce the waves. But a powerful muscular effort need not engage the entire attention, for it is possible to listen to the rhythm whilst the effort is made.

THE CORTICAL MECHANISM OF THE RHYTHM.

The general nature of the Berger rhythm seems to be fairly clear though several points are still obscure. We have to account for a

pulsating activity which develops in the occipital lobe and involves a considerable number of neurones working synchronously. These beat together with a fixed period, but they can only do so when pattern vision is absent.

Now synchronous activity can only occur in a group of neurones when the conditions of excitation are uniform throughout the group. When this obtains the neurones will all discharge at the same frequency and they may come to work in phase with one another as a result of their interconnection. For instance, the vertebrate retina (Adrian and

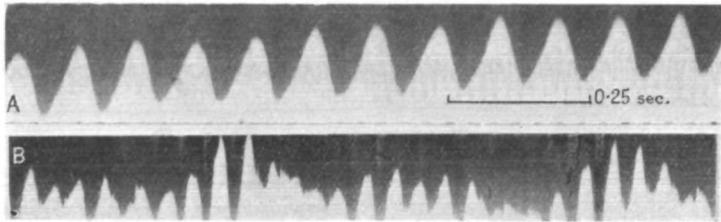


FIG. 12.—Records of potential changes from eye and optic ganglion of water-beetle (*Dytiscus marginalis*). Above, eye in the dark, waves at 9 a sec. Below, eye exposed to bright, uniform light, waves at 20 a sec.

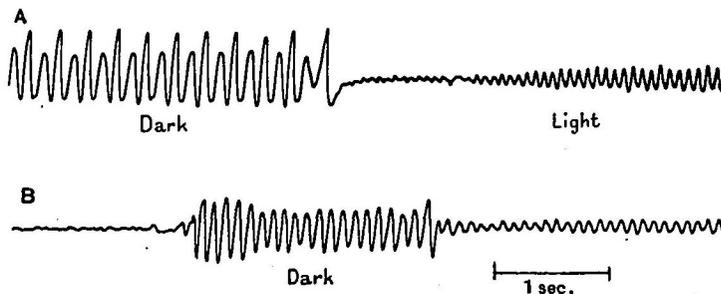


FIG. 13.—Eye and optic ganglion of water-beetle. Records showing the effect of different kinds of illumination.

- A. Eye in the dark and then exposed to bright, uniform light. Waves at 8 a sec. in the dark and at 14 a sec. in the light.
- B. Another preparation. Eye first exposed to medium non-uniform illumination (no waves), then in dark (waves at 10 a sec.), then to feeble non-uniform light (waves still at 10 a sec. but of much smaller amplitude).

R. Matthews, 1928) or the invertebrate optic ganglion (Adrian, 1932) may give a rhythmic electric pulsation when the eye is very brightly and uniformly illuminated and sometimes a rhythmic pulsation at a lower frequency when the eye is in darkness (fig. 12). In both conditions the neurones can pulsate synchronously because the degree of excitation is the same for all of them; but non-uniform illumination of medium brightness makes the synchronous beat impossible and abolishes the rhythmic potential waves (fig. 13).

The disorganization of a synchronous beat in the cortex is illustrated in fig. 14. This record is from the exposed brain of a rabbit under light urethane anæsthesia. The large waves represent periods of wide-spread activity due, probably, to the spontaneous discharge of the cortical neurones. At the signal the foot is pinched, and with the arrival of afferent impulses the cortical beat breaks up into small irregular

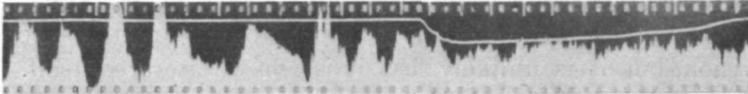


FIG. 14.—Potential waves from exposed cortex of rabbit under urethane. At the signal the foot is pinched and the waves break up into rapid asynchronous activity.

oscillations of high frequency—the sign of asynchronous action. The record is also an illustration of the general tendency for cortical neurones to discharge spontaneously when they are undisturbed. The cells of the respiratory centre give the best example of a spontaneous beat, but the cortical neurones are equally unable to remain for long without discharging, and electrical records show them to be in constant activity as long as they are supplied with oxygen.

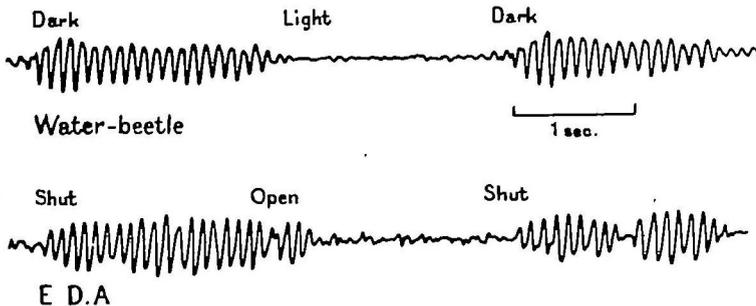


FIG. 15.—Comparison of waves from water-beetle preparation in darkness and light (upper record) and from human subject (E. D. A.) with eyes closed and open (lower record). In both the rhythm is abolished during visual activity.

The Berger rhythm has a fixed, low frequency, and appears in or near the visual part of the cortex in the absence of visual stimulation. Thus it most probably represents a spontaneous beat in a group of cortical neurones, a beat comparable to that of the water-beetle eye in darkness. There is, in fact, a surprisingly close resemblance in the records from man and from the water-beetle, for the frequency of the spontaneous beat happens to be much the same in both (cf. fig. 15).

The abolition of the rhythm by pattern vision represents the change from synchronous to asynchronous action; this would follow from the disturbing effect of a mosaic of excitations in the optic tract. In the same way the invasion of the beating area by widespread cortical excitations would prevent synchronous action although the visual field was uniform, and this would account for the effect of intense non-visual activities.

The difficulties begin when we attempt to decide the exact position and function of the area. It is in the occipital lobe and it is concerned with vision, but it is unlikely that it is the striate area itself. Many investigators have recorded the electric responses of the striate area and found the most prominent to be a large potential change when the eye is illuminated and another when it is darkened. With electrodes arranged on the head for recording the Berger rhythm there is no "on" and "off" effect of this kind, and indeed the position of the striate area makes it unlikely that potentials arising in it could be detected through the skull.

The area seems to have little or nothing to do with the perception of light, for the period of the waves is not altered by a change in the amount of light falling on the closed lids and the subject can notice the change without abolishing the rhythm. The area is not concerned with visual imagery, for the rhythm is unaffected by visualizing shapes, figures, &c. It is concerned with pattern vision, but the rhythm can be abolished by attempting to see a pattern as well as by the sight of one.

This complicates the issue by giving us two possible factors which may interfere with the synchronous beat. The absence of the rhythm when the eyes are first opened in a dark room seems to depend not on inequalities in the field but on the direction of a certain amount of attention to it. It is possible, therefore, that a pattern in the field abolishes the rhythm because it attracts the attention and not because it excites the area unequally. This, in fact, is the explanation given by Berger. The effectiveness of a pattern in abolishing the rhythm seems to depend entirely on the amount of sharp contrast in the central part of the field, but it is arguable that this determines the amount of attention which the pattern will attract.

The point is not worth elaborating until we have some idea of the neural processes which may be involved in attention. It is clear, however, that the area which gives the rhythm is concerned specifically with visual activities and is not some general correlating centre. As

was pointed out on p. 371 the visual activities which abolish the rhythm do not claim more than a small part of the subject's attention and if pattern vision is absent the rhythm persists in spite of other activities which demand a fair share of attention for themselves. It is clear, too, that the part of the brain concerned with vision would be the most likely place for a spontaneous beat covering a wide area. By shutting the eyes we can cut off the stream of impulses which enter the occipital lobe from the million fibres of the optic nerve. The visual areas of the cortex will be suddenly cut off from afferent excitation and left to themselves will be free to beat spontaneously. There is no other part of the brain in which so large an area could be so readily isolated from external influence, for vision is not only our most important sense but it is the only sense which can be turned on and off at will. It may be added that man is the animal most likely to show the Berger rhythm, for it is in man that the visual part of the brain reaches its highest development.

We have assumed that the area is so much a part of the visual apparatus that when vision is cut off there will be nothing left to disturb it. But an intense activity in the rest of the brain will do so, and it seems that if vision is permanently cut off the area is not allowed to remain idle but becomes gradually more and more accessible to excitations from other parts. In the end it will be continually disturbed and will have no chance of developing a synchronous beat. Thus the Berger rhythm is absent in the blind.

POTENTIAL CHANGES IN THE EXPOSED CORTEX.

It has been pointed out that the potential changes which can be recorded from the surface of the head in man bear little resemblance to those from the exposed cortex in animals. This may be due partly to the greater importance of vision in human behaviour and the greater size of the visual regions in the human brain. In cats and rabbits, for instance, the area which corresponds to that giving the Berger rhythm in man is certainly much smaller if it exists at all. It will therefore be much more exposed to disturbing effects from the neighbouring cortex and these may always prevent the spontaneous activity of the cells from developing into a synchronous beat.

There is, however, another reason for the different character of the records from animals, namely that these are made with electrodes leading directly from the exposed cortex, whereas in man the electrodes are separated from the cortex by the high resistance of the skull. This

arrangement is equivalent to one without the high resistance layer but with the electrodes at a much greater distance from the surface of the cortex. It can give a bird's-eye view, so to speak, of the cortical activity, showing the average potential changes of large areas but nothing of the local detail. With electrodes on the cortex the local detail has much greater prominence and may fill the picture to the exclusion of the general view. Thus surface electrodes on the forehead and vertex can record the Berger rhythm due to widespread pulsation in the occipital lobes, but cannot show anything of the more localized activities taking place in the brain immediately beneath them. On the other hand electrodes on the exposed cortex may show such large potential changes due to local activity that the Berger rhythm would have no chance to appear.

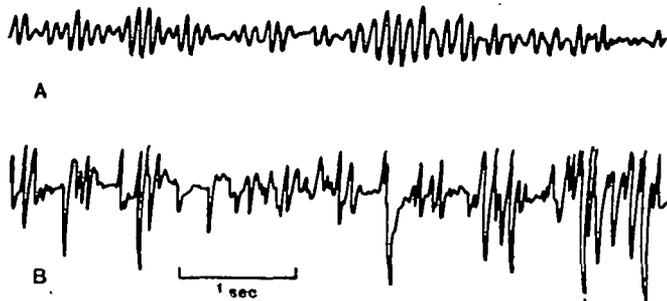


FIG. 16.—Records from the exposed cortex of a patient during an operation for removal of a tumour. A, before removal, cortex œdematous, typical Berger rhythm. B, after removal of tumour and recovery of circulation in the cortex, large irregular waves (the oscillograph is shunted to one-fourth of its former sensitivity).

This may be illustrated by some observations made on the exposed cortex of a patient of Mr. Cairns, who very kindly allowed us to take records during an operation. The patient was a woman with symptoms of a tumour in the right parietal region. When the skull was opened (under local anæsthesia) the exposed cortex was œdematous and the vessels congested. At this stage thread electrodes on the surface of the cortex showed the Berger rhythm and nothing else (fig. 16, A). Mr. Cairns then removed a large neoplasm which infiltrated the cortex in front of the area we had examined. After the removal and about one and a half hours after the first record the electrodes were replaced on the cortex. The œdema and congestion had disappeared and the vessels pulsated well. The record now showed no sign of the Berger rhythm but instead was made up of much larger, irregular oscillations,

like those which can be recorded from the exposed cortex of a cat or rabbit (fig. 16, B).

The obvious explanation of these results is that when the first record was taken the cortex under the electrodes was completely inactive and behaved like so much inert connective tissue. Electrodes on it picked up the Berger rhythm as they would have done if they had been applied to the scalp outside. But with the recovery of the circulation the cortex regained its normal activity, and so at the second recording the local action potentials were so large that the Berger rhythm had no chance of showing itself.

It is clear that further work on the exposed cortex is needed to give a completely satisfactory account of the rhythm. Some uncertainty will remain until it has become possible to localize the beating area, to compare its reactions with those of the striate area, &c. Unfortunately the occipital region in man is very seldom exposed; for the present therefore all that can be said is that records from the exposed brain do not conflict with the view that the rhythm arises in the occipital cortex.

THE RESPONSE TO FLICKER.

The foregoing account of the mechanism of the Berger rhythm is supported by the discovery that regular potential waves at frequencies other than 10 a second can be induced by flicker. If a group of cells tends to beat spontaneously it should be possible to induce a beat at a higher rate by rhythmic stimulation. Accordingly we have tried recording the potentials from the head when the eyes are exposed to a flickering field, and we find that it is possible in this way to obtain rhythms as high as 25 a second.

To produce the response the flicker must involve a considerable part of the visual field. If it is limited to the central part of the field the potential changes are as small and irregular as they are with pattern vision. In the arrangement we have used the subject sits as in fig. 9 with the eyes at the centre of an opal glass bowl and the head covered by a black velvet curtain. The convex surface of the bowl is lit by a 30-watt headlight bulb placed 12 in. away behind a sector wheel, 2 ft. in diameter, rotated by a gramophone motor. The sector wheel gives eight light and eight dark intervals of equal length in each revolution. As the speed at the periphery is high and the distance from the filament very small, the light or shadow takes an inappreciable time to spread over the bowl. The field is brighter at the centre than at the periphery, but unless patterns are deliberately introduced it is uniform enough to allow

the Berger rhythm to develop with the eyes open and the light steady.

Typical records of the response to flicker are given in fig. 17. At the beginning there is the usual 10 a second rhythm, for the eyes are closed and the light is cut off by a shutter. At a signal the eyes are opened and the shutter lifted to turn on the flickering light. The result is a series of potential waves having the same frequency as that of the flicker.

To obtain this result the intensity of the light has to be carefully adjusted. If it is too dim the sensation of flicker soon dies away and the rhythm reverts to 10 a second. If it is too bright the field may become filled with coloured patterns, the sensation is extremely

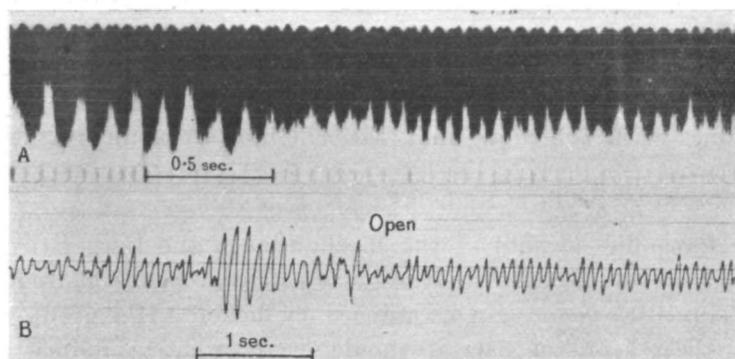


FIG. 17.—Potential waves produced by exposing the eyes to a uniform flickering field. Each record begins with the eyes closed to show the usual 10 a sec. rhythm.

- A. E. D. A. Flicker at 16 a sec.
 B. C. L. P. Flicker at 14 a sec.

unpleasant and no regular waves are obtained. But it is usually possible to find an intensity which will at the worst give occasional patches of the flicker rhythm; more often the rhythm is clearly marked when the eyes are first opened and becomes intermittent after a time, but is never absent for more than a second or two.

Controls have been made to ensure that the potential waves are not artefacts due to induced effects from the sector wheel or its motor or to the flickering light acting directly on the electrodes. The latter possibility is ruled out by covering the head with several layers of black velvet to exclude any stray light which might reach the electrodes. The wheel and motor are not responsible as they are kept running throughout the experiment, whereas the rhythm only appears when the eyes are open. It can be shown also that the potential waves of the

flicker response come from the same part of the head as the waves of the Berger rhythm, for the relative sizes of the two remain the same when the position of the electrodes is changed, although the absolute size varies greatly (fig. 18). This does not prove that they arise from

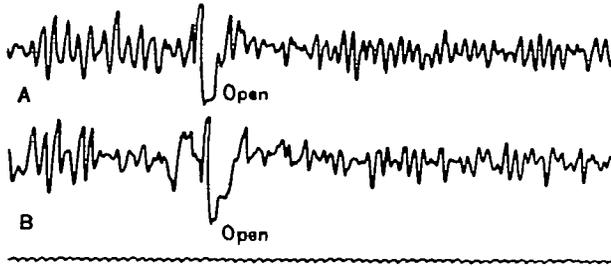


FIG. 18.—Records showing that the relative size of the waves of the Berger rhythm and of the waves due to flicker remain the same for different positions of the electrodes. Subject E. D. A. Signal line shows frequency of flicker.

- A. Electrodes on vertex and occiput. Half way through the eyes are opened to a field flickering at 14 a sec.
- B. Electrodes on forehead and vertex. Sensitivity increased to make the waves of the Berger rhythm equal to those in record A. Eyes opened to flickering field as in A.

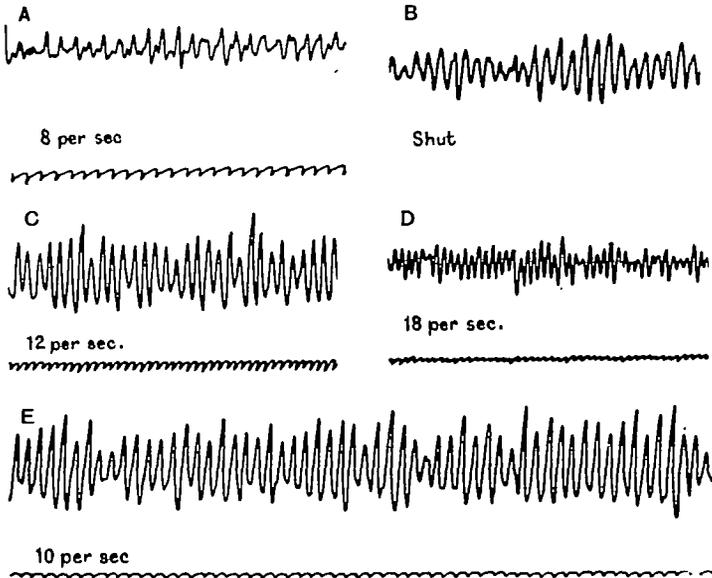


FIG. 19.—Examples of different rhythms induced by flicker. Subject E. D. A. Signal line shows frequency of flicker.

- A. Flicker at 8 a sec.
- B. Eyes closed and field dark. Berger rhythm at 10 a sec.
- C. Flicker at 12 a sec.
- D. Flicker at 18 a sec.
- E. Flicker at 10 a sec. Compare with B.

exactly the same area but shows at least that the flicker response must come from the occipital lobe, if the Berger rhythm does so. The existence of the flicker response may be taken as an additional argument against the view that these potential changes are due to eye movements. There is certainly no visible oscillation of the eyeball when the response is present: a tremor of the external ocular muscles is possible, but the evidence on p. 359 shows that this could scarcely account for the potentials.

The flicker rhythms are shown most clearly with rates between 10 and 20 a second (fig. 19). We have not tried rates higher than 25 a second as the apparatus could not be run comfortably at higher speeds. With rates between 7 and 10 a second the flicker rhythm is sometimes

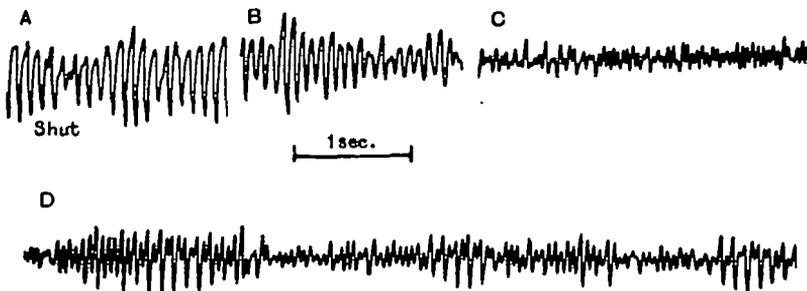


FIG. 20.—Rhythms of double and half the rate of the flickering light. Subject K. Y.

- A. Eyes closed, field dark. Berger rhythm at 10·5 a sec.
- B. Flicker at 12 a sec. Waves at the same rate.
- C. A few seconds later. Waves now at 24 a sec. with occasional reversion to the 12 a sec. rhythm.
- D. Flicker at 18 a sec. Large waves at 9 a sec.

quite clear, but the intensity of the light needs careful adjustment. With flicker in the neighbourhood of 20 a second there is in some subjects a tendency for the waves to occur at half the rate (fig. 20, D). More rarely the rhythm becomes twice that of the flicker, though only for short periods at a time (fig. 20, C).

When the flicker is in the neighbourhood of 10 a second the results are unexpected, for it is, if anything, more difficult to obtain a regular series of waves. If the flicker rate is slightly slower or faster than the Berger rhythm there are often periods of complete irregularity, but if the rate is adjusted very carefully in the hope of making it coincide exactly the waves may become extremely regular and may continue for many minutes without the usual waxing and waning in size. The subject is not conscious of any change in sensation when the regular

wave train appears. A sample of the rhythm produced in this way is given in fig. 19, F, with a sample of the normal Berger rhythm (with eyes closed) from the same subject. As a rule the waves of the flicker response have less rounded contours besides being more uniform in size. The need for careful and prolonged adjustment of the flicker rate suggests that the rhythmic excitation plays on the area in a way which must antagonize the spontaneous beat until a particular phase relation is established. The position is perhaps comparable with that of the auricle stimulated electrically at a rate so close to that of the pacemaker that the beats sometimes come from the extrinsic or sometimes from the intrinsic focus.

Whatever the explanation of this may be, there is no doubt that when once the 10 a second flicker rhythm is established it can resist disturbing influences which would upset the spontaneous beat. The central part of the field need not be uniform—the subject can look at a black cross drawn in the centre of the opal screen, seeing its outlines clearly, and he can solve problems in mental arithmetic which would certainly abolish the Berger rhythm. To some extent this is true of the flicker response in general, but at the higher rates pattern vision, &c., usually causes some reduction in the size of the waves. The greater stability of the flicker response is natural enough: with flicker a co-ordinated beat is imposed on the area by the rhythmic excitation, whereas with the spontaneous waves there is nothing but their own interaction to synchronize the different neurones.

It is perhaps remarkable that the area can be excited rhythmically by the flicker, when it seems to be unaffected by a single change in the degree of illumination in the field. It would be easier to explain the cortical mechanism if a steady bright field gave a faster rhythm than a dark field, as it does with the response of the optic ganglion (cf. fig. 12), but the fact remains that the rate can never be altered by changing the light intensity unless the changes are repeated very rapidly. Apparently the area is not concerned with the perception of light, but is near enough to the striate region to be affected by a rhythmic pulsation there.

DISCUSSION.

If the Berger rhythm represents a spontaneous beat of a group of neurones, it is not surprising that the frequency is much the same in all individuals and under all conditions. Unless a different rhythm is imposed by flicker the synchronized beat can only occur when the

neurones are undisturbed ; the rate of beating will then depend on the constitution of the cells and on nothing else. Thus the Berger rhythm is disappointingly constant, for it expresses time relations which are determined by the fundamental properties of the cells.

Berger has investigated the rhythm in a very large number of subjects in different conditions, e.g. sleep, anæsthesia, drug intoxication, &c., and has reported certain instances of a slow rate associated with pathological states of the brain, but in normal subjects the rate is seldom less than 9·5 or greater than 10·5 a second. There are, however, considerable variations between one subject and another in regard to the persistence of the rhythm and the fluctuation in the size of the waves. One of us (E.D.A.) gives the rhythm as soon as the eyes are closed, and maintains it with rare and brief intermissions as long as they remain closed. The other (B.H.C.M.) is better in the role of observer than of subject, for in him the rhythm may not appear at all at the beginning of an examination, and seldom persists for long without intermission. In another subject an extremely uniform series of waves appear suddenly 10 seconds or more after the eyes are closed, the record giving the impression that the beat is harder to achieve but more perfectly synchronized when once it has developed. There are also considerable variations between individuals in the ease with which the flicker response can be obtained, in the tendency to give waves at half the flicker rate, in the amount of pattern which can be tolerated in the visual field, &c.

There is no evident connection between these features and any of the known physical or mental traits of the different individuals, but we have not been specially concerned to detect any correlation, since our main problem has been the neural mechanism of the rhythm. Our explanation of it differs considerably from that given by Berger and until its nature is agreed upon the study of individual differences cannot lead very far. If we have not misunderstood his writings, Berger's view of the rhythm is that it represents the normal activity of every part of the cortex; afferent stimuli which claim the subject's attention will cause a more intense local pulsation, but will inhibit the beat over the rest of the brain, with the result that the waves can no longer be detected outside the skull, and visual stimuli are particularly effective in inhibiting the beat since vision plays the most important part in controlling the work of the brain. The evidence of localization and the rhythms induced by flicker seem to us to be definitely opposed to this view. It is possible, however, that the disappearance of the rhythm is sometimes due to

inhibition rather than to the change from synchronous to asynchronous action. Both processes would suppress the beat and our only reason for preferring the latter is that it operates in other examples of nervous rhythm which have at least a superficial resemblance to the Berger phenomenon.

The resemblance to the beat of the retina or of the optic ganglion of insects would have been overwhelming if it had turned out that the Berger rhythm originated in the striate area. As it is, the absence of an "on" and "off" effect and perhaps also the failure to alter the frequency by changing the illumination of the field show that the rhythm is not strictly comparable to that of a pure receptor mechanism like the retina. The suppression of the rhythm by trying to see in the dark is another fact for which there is no certain explanation, though the change from synchronous to asynchronous activity is as likely as any other. But the Berger waves would add very little to our knowledge if everything could be explained so simply. Their greatest interest lies in their relation to the organized activities of the cerebrum. Berger has stressed the importance of the rhythm as a possible clue to the neural mechanism of attention and our failure to agree with his view of its origin does not lessen its interest in this respect.

It is true that, in our view, the rhythm shows the negative rather than the positive side of cerebral activity; it shows what happens in an area of cortex which has nothing to do, and it disappears as soon as the area resumes its normal work. This is almost inevitable, for to give potential waves which can be detected through the skull a considerable area must beat synchronously and it is unlikely that this could occur in any region which was taking an active part in coordinating incoming and outgoing messages. The rhythms induced by flicker represent a positive activity, but one which cannot often occur normally. It is unlikely, therefore, that records made with the skull intact will give detailed evidence of the normal positive activity of different regions of the brain. The Berger rhythm shows the background of spontaneous discharge, but it can also show when that background is obscured and this may be information well worth having, from the practical as well as the theoretical aspect.

SUMMARY.

The paper deals with Berger's discovery that regular potential oscillations at 10 a second can be detected in the human subject by electrodes applied to the scalp. Berger's conclusion, that the waves are

due to the electrical activity of the cortex, is confirmed, but evidence is given to show that they arise from an area in the occipital lobes connected with vision, and not from the whole cortex. The distribution of current in the scalp indicates that the focus of maximum activity, though confined to the occipital region, can change its position from time to time.

The essential condition for the appearance of the Berger rhythm is that pattern vision should be absent. It develops when the eyes are closed or if the visual field is uniform, and disappears whenever the central part of the field has any detail. The attempt to see detail, even though the field is uniform, abolishes the waves: for this reason the closure of the eyes, by withdrawing the attention from visual phenomena, aids the development of the rhythm. Its frequency is not altered by changing the illumination of the field, and it is not abolished by the perception of light and darkness or by visual imagery. In patients who have been blind for some years we have not been able to detect any trace of the rhythm. As Berger has shown, non-visual activities which demand the entire attention (e.g. mental arithmetic) abolish the waves; sensory stimuli which demand attention do so too.

We believe that the potential waves are due to the spontaneous beat of an area in the occipital cortex which is normally occupied by activities connected with pattern vision. When the area is unoccupied the neurones discharge spontaneously at a fixed rate (as in other parts of the central nervous system) and tend to beat in unison. Visual activity and widespread non-visual activity break up the synchronous beat by exposing the area to non-uniform excitation. In man a large area is normally occupied with visual activities; thus when the area has nothing to do and is free to develop a synchronous beat the potential changes are large enough to be detected outside the skull. It appears that the area does not remain permanently unoccupied if vision is lost; in subjects who are blind it must have become more accessible to the rest of the brain.

The close relation of the area to the visual mechanism is confirmed by the fact that the frequency of the rhythm can be altered by exposing the eyes to a uniform field which flickers at varying rates. The waves then tend to occur with the same frequency as the flicker. The frequency of the spontaneous rhythm varies within narrow limits in different subjects, but there is much individual variation in the persistence of the rhythm, uniformity of the waves, &c.

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