NOTE ON THE PHYSIOLOGY OF THE BASAL GANGLIA AND MID-BRAIN OF THE ANTHROPOID APE, ESPECIALLY IN REFERENCE TO THE ACT OF LAUGHTER. By T. GRAHAM BROWN.

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Introduction. The question of the higher centres which control the respiratory centre in the medulla oblongata is one of interest. It is obvious that such centres exist. For instance, the act of respiration may be stopped in a "voluntary" manner for a short space of time. This seems to point to a cerebral control of respiration. Again, the normal respiration is greatly altered in many acts—for example that of laughter—which are supposed to be the expression of activities of centres higher than those of the mid-brain. Indeed the act of laughter may be looked upon in great part simply as an alteration of the act of breathing. Now it is generally assumed that the act of laughter is one conditioned by centres which lie in the neuraxis above the level of the anterior corpora quadrigemina. If this is the case there must be centres above this level which in their activity have an influence upon the lower respiratory centres.

It is perhaps not going too far out of the line of this present paper to notice a curious parallel which may be drawn between the relation on the one hand of the scratch-reflex to progression and that on the other hand of the act of laughter to the act of normal respiration. In either of these two relationships what we may term the fundamental acts—progression and respiration—are comparatively slow rhythmic movements. They seem to be peculiarly susceptible to the "blood-stimulus" factor in their conditioning (when that term is used in its widest sense). They are conditioned greatly (but not fundamentally) by proprio-ceptive self-generated stimuli—in the one case by the proprio-ceptive stimuli from the receptive end-organs in the muscles of the limbs, and in the other case by the proprio-ceptive stimuli from the receptive end-organs in the lungs. In either case the rhythmic act shows great persistence when subjected to the chemical narcotic and then exhibits the peculiarity of the apparent one-sidedness of an otherwise double act. Thus progression is normally conditioned by a rhythmic alternation of extension and flexion. The flexion is produced by the contraction of the flexor muscles; the extension is conditioned in part by the action of gravity on the limb (thus producing a passive relaxation of the flexor muscle) and in part by the active contraction of extensor muscles. But in the phenomenon of "narcosis progression" the rhythmic activity seems to occur in the absence of movement of any kind in the extensors—it is conditioned solely by contraction and relaxation of the flexors[1]. In a similar manner respiration is conditioned by the alternation of inspiration and expiration. Of these acts inspiration is produced by active contraction of inspiratory muscles (= flexors ?) and expiration is produced by the action of gravity (in man) and the elastic recoil of the chest wall either alone or in conjunction with the active contraction of expiratory muscles. In respiration under narcosis, and even in the normal respiration of the mammal which is not undergoing great exercise, the expiratory muscles do not take part in the act of respiration. In the case either of respiration or progression the rhythmic act is greatly influenced by the establishment of a state of asphyxia. In either case extero-ceptive stimuli may alter the progress of the rhythm—the spur in the case of the progression of the horse, a douche of cold water in the case of respiration. And finally in either case the rhythm may be stopped and started again by a change in the state of the cerebral centres—"voluntarily." In the two relationships which we are about to consider a close parallel may therefore be drawn between the fundamental rhythmic activities.

If now we take the first relationship—that between the scratch-reflex and progression—we find that in the two rhythmic acts the same

[1] *Proc. Roy. Soc.*, B, LXXXVI. p. 140. 1913. This *Journal*, XLVIII. p. 18. 1914.

muscles of the limbs take part. The rate of the rhythm of their movements is however considerably greater in the scratch-reflex than in progression. They act reciprocally—the flexor contraction being accompanied by extensor relaxation and *vice versa.* A curious point is the apparent greater persistence of extensor activities in the scratch-reflex than in progression. It is at present not possible to say that the scratch-reflex cannot occur in flexor muscles alone—that when it occurs both sets of antagonists are active—but at any rate in the scratching movements which occur in the guinea-pig under narcosis the extensors are active. The progression phenomenon seems to be conditioned (in certain circumstances) by the activity of the lower spinal centres alone. Thus it may be conditioned by the lumbar centres after their functional separation from the higher parts of the neuraxis. But the scratch-reflex seems to be conditioned by a centre (or by centres) in the higher part of the spinal cord, and these centres seem to act through the same lower centres which control the act of progression. In the case of progression the fundamental condition appears to be the equivalent of the "blood-stimulus" in respiration[1], and a great (although secondary[2]) condition is the phasic self-generated series of stimuli from the proprio-ceptive end-organs in the muscles of the limb. While the proprio-ceptive factor no doubt plays a part in the scratch-reflex the fundamental condition may be regarded not as this nor as the "blood-stimulus" but as the extero-ceptive stimulus from the skin end-organs round the hairs of the trunk and head. Indeed the scratch-reflex might be looked upon as due to a modification of the act of progression conditioned under the influence of the activity of cutaneous end-organs. The effect of this activity may be reproduced by the artificial stimulation of the afferent nerves which proceed from these end-organs—for example, by the electrical stimulation of the cut ascending branches of nerve fibres in a cross-section of the cervical spinal cord. Finally the act of scratching, as must be within the experience of all of us, is accompanied by psychical states. We have the feeling of pleasure and satisfaction. In other words there is an emotional accompaniment of the act, whereas progression is usually sub-conscious.

Proceeding now to the second relationship—that between the acts of laughter and of respiration—we find that it has many similarities to the first. The same muscles take part in the two acts (laughter and respiration). The movements are rhythmic, but the rate of the rhythm

[1] *Proc. Roy. Soc.*, B, LXXXVI. p. 140. 1913. This *Journal*, XLVIII. p. 18. 1914.
[2] *Proc. Roy. Soc.*, B, LXXXIV. p. 308. 1911.

is greater in laughter than in normal respiration—just as it is greater in the scratch-reflex than in progression. Nevertheless the rate of respiration may in certain circumstances approach that of laughter—just as, under the influence of asphyxia, the rate of progression may approach that of the scratch-reflex[1]. Again a point of interest is the activity of the expiratory muscles (= extensors ?) in laughter, whereas in normal respiration they play no part or a very slight one. Respiration appears to be conditioned by centres which lie in the medulla oblongata—that is, high spinal centres; but laughter seems to be conditioned by centres higher than these. It is possible that a parallel may be drawn between the lower progression centres and the higher scratch-reflex centres on the one hand and the lower respiratory centres and higher laughter centres on the other hand. In the case of respiration the fundamental condition seems to be the "blood-stimulus," while the phasic self-generated proprio-ceptive stimuli from the lungs seem to play a great but a secondary part. But in the case of laughter the chief condition appears to be the activity of extero-ceptive end-organs—as in the case of the scratch-reflex. Thus laughter may be evoked by auditory or visual stimuli, or by the memories of auditory or visual images (in which cases perhaps the equivalent of the "blood-stimulus" may play a part), and above all it may appear under the influence of the cutaneous extero-ceptive stimulus of "tickling." Here there appears to be a very close parallel between laughter evoked in this manner and the normal scratch-reflex; while a parallel to the laughter produced by memories of visual and auditory images is perhaps to be found in the phenomenon of "narcosis scratching." It is possible, as will be described in this paper, that a form of laughter equivalent to that evoked by tickling may be evoked by the artificial stimulation of certain parts of the neuraxis—just as the scratch-reflex may be. Finally, respiration is a sub-conscious act and is not normally accompanied by an emotional state. But laughter has a strong psychic concomitant—a feeling of satisfaction and pleasure perhaps equivalent to that which accompanies scratching.

These parallels may seem to be too far fetched, but at any rate it must be admitted that there are grounds for the suggestion (it is no more) that the act of laughter may bear a similar relationship to the act of respiration as that borne by the act of scratching to the act of progression; while there are strong grounds for the parallel between the act of respiration and that of progression.

[1] *Proc. Roy. Soc.*, B, LXXXVI. p. 140. 1913.

In the experiment here described the possible effect upon the act of respiration of artificial stimulation of certain areas in the cross-section of the neuraxis at and above the level of the anterior colliculi was investigated in the anthropoid ape. In a short preliminary communication[1] it has already been shown that artificial stimulation applied in the uni-polar method to certain points in the cross-section of the mid-brain of the monkey at the level of the anterior colliculi may evoke changes in the act of respiration.

Methods. The animal used in these observations was a large male chimpanzee—*Troglodytes niger*—which was in rather poor condition. After a series of investigations into the function of the cerebral cortex under the influence of a chemical narcotic the animal was decerebrated by division through the neuraxis a little in front of the anterior colliculi (see Figs. 1, 3). The actual plane of division was not quite at right angles to the axis of the central canal (aqueduct of Sylvius). On the dorsal aspect of the neuraxis it passed about 3 mm. in front of (oral to) the anterior boundary of the anterior colliculi. The plane of section then passed somewhat backwards so that its ventral part cut through the mid-brain at the level of the centre of the anterior colliculi. Thus the plane of section passed through the optic thalamus above and through the mid-brain below—the upper third of the surface being composed of thalamus. The section passed almost immediately in front of (oral to) the posterior commissure. Later a second trans-section of the neuraxis was performed. This was in the mid-brain and the plane of division passed through the middle of the anterior colliculi on the dorsal aspect of the neuraxis and exactly through the anterior (oral) boundary of the pons Varolii on the ventral aspect. The depth of narcosis during the first of these lesions was so great that respiration failed for a time and the animal had to be kept alive by artificial respiration. Thereafter normal respiration became re-established.

Different points on the exposed surface of the first cross-section were stimulated artificially by means of rapid induced electrical currents applied in the uni-polar method—the indifferent electrode being bound upon one of the feet. Later in the experiment the second cross-section was stimulated in a similar manner, but the animal was then dying and the results obtained were few in number. It is scarcely necessary to state here that the animal was completely unconscious throughout the whole of the experiment and until it died at the end of it.

[1] *Proc. Physiol. Soc.* p. xxxii. 1914. (This *Journal*, XLVIII.)

I. *Note on the act of laughter and other expressions of emotion in the chimpanzee.*

The following observations, which have a bearing upon the experiments about to be described, were made upon another and a young male chimpanzee at present in the laboratory. This animal is (March, 1915) 30 or 31 months old. We have had it in the department for about 18 months. At first it was extremely wild, but is now very tame. It shows no evidence of fear—even for instance when a lighted match is held before its face—except when a stranger comes into the room.

When thus excited the ape screams violently, showing its teeth in the manner common in chimpanzees in such circumstances. When happy it protrudes its lips and gives the "Ou, Ou, Ou" cry. If it is feeling lonely it whimpers when we leave the room—the sound being similar to the moan of a child, but not to the child's sobbing which we have not observed in this individual. If this cry does not die away it developes into the scream.

The chimpanzee may be tickled by rubbing the skin in the hollow of the shoulders, in the arm-pit, and between the scapulas. In the latter case the back is straightened, the head is thrown back by an extension of the neck, and the lips are retracted. This retraction differs from that seen when the animal screams. It may at first be slight, but later of greater extent. It is best described as a smile. At the same time the respiration becomes more rapid and slightly vocal. The sound given is that of "Ha, Ha, Ha," but not *said* as we say it—rather whispered. There can be little doubt that this reaction to tickling is equivalent to the act of laughter. Of late, with the increasing tameness of the animal, it has become more difficult to obtain reactions to tickling.

II. *Stimulation of the pyramidal tract area.*

In the decerebrate chimpanzee investigated in these observations the lower part of what has been termed the first cross-section of the neuraxis in the description of methods used was formed by the pyramidal tract (see Figs. 1, 2).

Uni-polar stimulation of the right pyramidal tract yielded movements of the contralateral (left) limbs. Movements of the ipsilateral limbs were not observed. In the case of the left arm these movements were examined in two isolated antagonists—*supinator longus* and

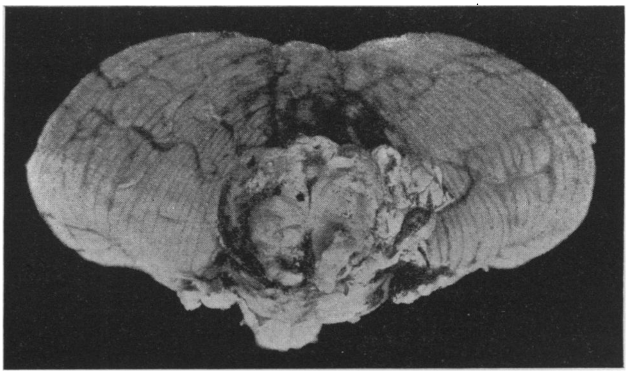

Fig. 1. Photograph (life-size) of the oral aspect of the mid-brain and cerebellum of the anthropoid ape the examination of which is described in the text. The cut surface of the mid-brain is that exposed after the first transverse lesion. The upper part of the exposed surface is really composed of optic thalamus, the lower part of mid-brain. The central canal of the neuraxis (here the caudal end of the third ventricle) is clearly shown, and the posterior commissure is also distinctly to be seen.

The three black dots on the right side of the exposed cut surface were not drawn upon the photograph—which is untouched. They are indian ink marks which were placed upon the surface of the mid-brain during the experiment and they correspond very accurately to the centres of the "focal" areas described in the text.

In the next figure an outline drawing of this photograph is given.

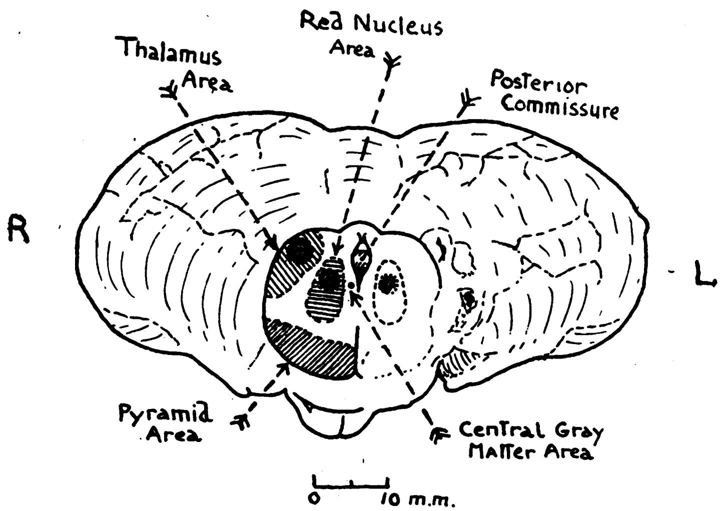

Fig. 2. Outline drawing of the preceding figure. On the right side of the cross-section of the neuraxis are drawn three shaded areas. These are: the pyramid area below,

the red nucleus area in the centre, and the thalamus area above and to the side. In addition the small point near the mid-line (central grey matter area) is also shown.

Within the red nucleus area and the thalamus area the "focal" areas are shown by darker shading. That for the red nucleus area is also shown more clearly upon the left side of the cut surface. These areas were carefully drawn upon a sketch map during the experiment. That map has been corrected against the photograph and the areas here represented may be regarded as approximately exact. Of course it must be noticed that the "spread" phenomenon of the exciting electric current makes it possible that the area from which a reaction is apparently evokable may not correspond exactly with the anatomical structure stimulated. Thus the responsive area will almost certainly be larger than that of the structure.

The unshaded areas on the right side of the surface of the cross-section are "dead areas." Moderate uni-polar stimuli of strengths sufficient to evoke reactions from the shaded areas failed to evoke reactions from the unshaded ones.

triceps after the destruction of its scapular head. Flexion (flexor contraction, extensor relaxation) was the only movement which could be evoked at the elbow-joint.

Passing upwards on the surface of the cross-section (that is, passing towards the dorsal aspect of the neuraxis) it was found that immediately dorsal to the pyramidal tract area there was a "dead" or "silent" area. In other words there was an area from which no obvious reactions of the carcase of the animal could be evoked by uni-polar stimulation when the strengths of current used were those which were effective in the other (responsive) areas. When a strong stimulus was applied to this dead area reactions were evoked, but that stimulus was so strong that the results obtained were certainly due to "spread" of current stimulating the other areas.

III. *Stimulation of the area of the red nucleus.*

Immediately above (dorsal to) the "dead" area there was a responsive area which corresponded anatomically with the site of the *red nucleus*. This area was about 9 mm. long. Its long axis lay parallel to the mid-longitudinal dorsi-ventral plane of the neuraxis. In shape the area was almond-like, being of greater width below (ventral) than above. Its greatest width was about 5 mm. Its inner boundary lay about 2 mm. external to the mid-dorsi-ventral line of the neuraxis. The lower (ventral) two-thirds of this area lay upon the portion of the cross-section which was composed of mid-brain, while the upper third seemed to lie upon that portion which was composed of thalamus (Figs. 1, 2).

This area is that from any part of which moderate uni-polar stimulation evoked the characteristic red nucleus reactions[1]. Within it lay a "focal" area from which these reactions seemed to be peculiarly excitable. This focal area appeared to correspond with the ventral half of the dorsal half of the whole area—that is, with the second quarter of the whole area numbering from above (dorsal) downwards (ventralwards).

The reaction evoked on stimulation of this area consisted in flexion of the arm of the same side of the body; extension of the arm of the opposite side; rotation of the head to the same side of the mid-line. In this movement of the head the face sometimes appeared to be retained pointing straight forwards, but the neck was flexed to the same side as that stimulated. The movements of the lower limbs were not carefully examined. There however appeared sometimes to be extension of the lower limb of the same side of the body and flexion of that of the opposite side. In these movements all the joints of a limb took part. They were comparatively slow and well sustained and they tended to outlast the stimulus applied in a maintained postural after-discharge.

A more detailed analysis of the movements at a single joint of one of the arms has been described in another paper[2].

Surrounding this red nucleus area there was another "dead" area, except at a single small circumscribed point on its internal aspect. The strength of stimulus necessary for the evocation of the red nucleus reactions was greater than that which evoked reactions from the other responsive areas in this cross-section.

IV. *Stimulation of the grey matter round the neuraxial canal in the cross-section.*

Just internal to the red nucleus area opposite the central point of its long axis and between its internal boundary and the mid-longitudinal dorsi-ventral plane of the neuraxis there was a small and very strictly circumscribed area from which a peculiar reaction could be obtained on uni-polar stimulation (Figs. 1, 2).

This area itself was scarcely more than a millimetre across when liminal and even fairly moderate stimuli were used to localise it. It lay quite close to the mid-dorsi-ventral line—its inner margin being about 1 mm. or 0·5 mm. from that line; and it was about 3 mm. below (ventral to) the ventral edge of the posterior commissure. The area

[1] *Proc. Roy. Soc.*, B, LXXXVII. p. 145. 1913. This *Journal*, XLIX. p. 185. 1915.
[2] This *Journal*, XLIX. p. 185. 1915.

probably lay on the grey matter round the aqueduct of Sylvius or the third ventricle.

Weak uni-polar stimulation applied to this area at once evoked very rapid respiratory movements. The reaction was a most remarkable one. The normal slow, deep, and steady respiration suddenly changed to a fast and shallow breathing. Cessation of stimulation was not followed by a continuation of the fast breathing—it at once reverted to normal. The sound of this breathing was very similar to the "Ha, Ha, Ha" of the laughing chimpanzee. The abdominal muscles of both sides of the body appeared actively to contract and relax during the reaction.

The red nucleus area was irresponsive to stimuli of the strengths which evoked this reaction and also the reactions (about to be described) from the caudal pole of the optic thalamus.

A rise of blood-pressure was observed when this small respiratory area was stimulated. This rise was evidenced by the renewed bleeding of numberless points on the cross-section.

V. *Stimulation of the caudal pole of the optic thalamus.*

External to the red nucleus area there was another "dead" area, and external to that again there was a responsive area. This lay along the dorsal and lateral margin of the cross-section of the neuraxis in its upper two-fifths. The area was broader above (dorsal) than lower down, and its greatest breadth was about 4–5 mm. while its length was about 10 mm. Within it there was again a "focal" area. This, which was about 4 mm. in diameter, lay in the upper (dorsal) half of the area. The reactions evoked on stimulation of the different points within the whole area differed somewhat. The area itself lay on the part of the cross-section which was composed of optic thalamus. The cross-section here passed about 2–3 mm. oral to the caudal pole of the thalamus (Figs. 1, 2, 3).

Uni-polar electrical stimulation applied to the lower (ventral) part of this area gave a characteristic alteration of respiration. The breathing became very vigorous and "hollow"—the abdominal muscles taking part in the act. At the same time there seemed to be an increase of salivation.

From the middle of the area the reaction evoked appeared to resemble "sighing."

Stimulation applied to the upper (dorsal) part of the area, and especially to the focal area within it, gave a slowing of respiration—the movements being apparently those of "panting."

These reactions tended to outlast the stimulus which evoked them.

The strength of stimulus necessary to evoke these reactions was a comparatively weak one. With this strength of stimulus the red nucleus was irresponsive, and there was thus a "dead" area between this thalamic respiratory area and the small respiratory point near the mid-line from which rapid breathing was evoked.

VI. *Stimulation of the second (more caudal) cross-section of the neuraxis at the level of the mid-brain.*

The second cross-section passed through the middle of the anterior colliculi on the dorsal aspect of the neuraxis and through the caudal boundary of the mid-brain on the ventral aspect. Its plane was approximately at right angles to the mid-dorsi-ventral plane of the neuraxis (Fig. 3).

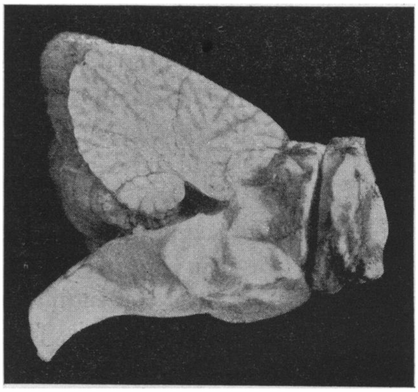

Fig. 3. Photograph (life-size) of the mid-brain and hind-brain taken from the right side after removal of the right half of the cerebellum for purposes of demonstration.

The portion of mid-brain enclosed between the first and second cross-sections of the neuraxis has been replaced and the photograph demonstrates the directions of the two lesions made in this experiment. Thus the first lesion is seen to start above (dorsal) through the optic thalamus about 3 mm. in front of (oral to) the oral boundary of the anterior colliculi. Below (ventral) it passes through the mid-brain at the level of the middle of the anterior colliculi. The second lesion passes above (dorsal) almost exactly through the centres of the two anterior colliculi, while below (ventral) it passes exactly between the oral boundary of the pons Varolii and the caudal boundary of the mid-brain.

Immediately after this section was performed the parts were left *in situ* and stimulation was again applied to the previously responsive points on the first cross-section. These were then found to be irresponsive and it must therefore be assumed that the results obtained from them immediately before the second lesion were in fact conditioned by the stimulation of structures which lay in the neuraxis between the planes of the first and second cross-sections.

Stimulation of the pyramidal tract area on the surface of the second cross-section gave results similar to those obtained on the stimulation of this area in the case of the first cross-section. So did stimulation of the red nucleus area. Alterations of the respiratory movements were not obtained, but the animal was rapidly dying. Such alterations would be expected to be obtainable.

Conclusions.

There can be no doubt that electrical stimulation of structures which probably lie in the caudal pole of the optic thalamus yields alteration of the respiratory movements.

The alterations thus obtainable have the characteristics of the similar alterations which, in the intact animal, we associate with emotional states. Such alterations are the "panting," "sighing," or "hollow" breathings seen in this experiment and, above all, the rapid "laughter" breathing.

The exact and circumscribed location of the area from which this last type of alteration of respiration was obtained suggests the presence there of a definite descending nerve tract. Perhaps this is identical with the fasciculus retroflexus of Meynert. In any case it is curious that this area should be separated from the larger area from which the other respiratory alterations were obtained on stimulation. It is possible that the "laughter centre" (if there is such a thing) lies higher in the neuraxis than the plane of the first cross-section made in this experiment, and that a descending tract has already become segregated at the level stimulated. It is, for instance, by no means improbable that such a "centre" might lie further oral in the optic thalamus.

The experiment gives definite proof of the connexion of the caudal pole of the optic thalamus with activities which condition reactions expressive of emotional states—reactions in which alterations of respiration and changes in blood-pressure play an important, if not a predominant, part. It is curious that such effective reactions can be obtained on stimulation of such circumscribed areas, and the method of investigation seems to offer to the future results of interest, but difficult to obtain because of the rarity and cost of the material necessary for their production.

One further point may be noticed. The reactions obtained are indicative of emotion, but it cannot be assumed that a concomitant of the electrical stimulation is the conditioning of the emotion with which in every-day life we associate the reaction. It is more probable that in this stimulation we are only activating a link in the chain of mechanisms which normally take part in the state. The movement of the tip of the tail of the cat is usually associated by us with the emotion of anger in that animal. But that movement may be evoked in the carcase of the spinal animal on appropriate stimulation of the cross-section of the neuraxis. In such a carcase we cannot believe that an emotion of anger exists, but its motor concomitant may be evoked by the stimulation of a lower part of the mechanism through which it is manifested. In a similar manner it is possible that in this present experiment the stimulus activates the motor mechanism at a lower level than that at which its activation is accompanied by the emotional state.