On Postural and Non-Postural Activities of the Mid-Brain.

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(Communicated by Prof. C. S. Sherrington, F.R.S. Received July 21, 1913.)

(From the Physiological Laboratory of the University of Liverpool.)

CONTENTS.

I. *Introduction.*

In the course of experiments in which the cerebral cortex of the monkey is stimulated, it is peculiarly noticeable that the activity of the cortex varies from time to time. That such variation should occur is by no means strange, in view of the difficulty of maintaining a constant depth of narcosis. But there are other variations which seemingly are not conditioned by

variation of depth of narcosis. Thus it not rarely happens that, when the depth of narcosis is certainly a constant one, the motor cortex becomes suddenly inexcitable. This occurs, for instance, after a cortical discharge, which is followed by "epileptic" after-discharge. But it also occurs without any apparent preceding cause. Thus suddenly the cortical excitability becomes abolished—at any rate, to practicable strengths of stimulation.

This sudden loss of cortical excitability is a phenomenon of interest. It is accompanied by two marked states. Of these, the first is an anæmia of the cortex; the second is a maintained postural contraction of certain of the muscles of the limbs. The anæmia seems to occur over the whole of the small area of cortex—pre-central and post-central—usually exposed in these experiments. It causes a sudden change in appearance from the "raw ham" look of the cortex when it is in the most favourable condition for electrical stimulation to a pale "dead" look. The cortex blanches; it may be surmised that it faints.

The postural contraction of the muscles of the limb have most carefully been examined in the case of the contralateral arm. In that member the posture is one of flexion. The contraction of the flexors is a great one, and it may be an exaggeration of the slight postural contractions (both flexion and extension) which the arm always exhibits in changing degrees throughout these experiments. But, from these muscular activities, this state of greater contraction must be carefully distinguished. For, in the former, cortical stimulation is effective, and can abolish or augment the postural contraction; but, in the latter case, the stimulation of the cortex is ineffective.

When this curious phenomenon is examined, two points stand clearly out. There occurs a postural activity of the flexor muscles of the contralateral arm, and this is accompanied by anæmia and by inexcitability of the cortex. The similar state of inexcitability which is seen after post-stimulatory cortical epilepsy is also accompanied by blanching of the cortex, and often by maintained posture of the arm.

From these facts the conclusion may be drawn that the postural activity of the limbs in this state is conditioned by the activity of certain of the lower centres. The question arises—which are these?

II. *Methods Employed.*

The animals used in the present experiments were small monkeys: *Macacus rhesus*, *Macacus sinicus*, *Callothrix*, *Cercocebus æthiops*. They were kept unconscious throughout the whole experiment, and until they were destroyed at its conclusion. The procedures of decerebration, removal of the cerebellum, etc., were performed in the usual manners.

Stimulation of the various parts of the neuraxis was performed in the unipolar method. Two unipolar electrodes were used in order that two points might be simultaneously

stimulated. These were on different circuits, and the two "indifferent electrodes" made necessary were applied one to either foot.

Stimulation of the peripheral nerves (ipsilateral and contralateral ulnars in the arm) was performed in the usual bipolar method.

For the proper examination of the movements of the arm in these experiments the movements of an extensor (humeral part of triceps brachii) and of a flexor (supinator longus) of the elbow were registered simultaneously. All the other muscles of the left arm and shoulder were destroyed by motor paralysis.

In the following descriptions the terms "ipsilateral" and "contralateral" are used in reference to the left arm—the former therefore meaning (here) "a point on the left side of the body," and the latter "a point on the right side."

III. *The State of the Monkey after Decerebration.*

After comparatively high decerebration (that is, when the neuraxis is divided across slightly anterior to the anterior colliculi), or even when the division is through the anterior colliculi, the animal is not perfectly immobile. When the depth of narcosis has shallowed the eyelids are open, and sometimes wide open. Winking frequently occurs, and the eyes sometimes are moved. From time to time the animal slowly changes its posture, the movements being like those of normal sleep. Owing to the fact that the animal in these experiments has been carefully covered and propped in a definite posture for the recording of the arm movements, it is not easy to describe those postures accurately. But, if the attention is confined to the movements of the left arm, it is seen that slow postural flexion and extension occur from time to time. The flexor thus may slowly contract, and, having reached its maximum of contraction, may there remain for many minutes if undisturbed. And, similarly, the extensor may at other times contract and remain contracted. The hind limbs may shew postural extension (Sherrington's "decerebrate rigidity") and, although the state of the hind limbs has not systematically been examined, it has seemed that they tend more frequently to demonstrate the extensor rigidity than do the fore limbs. From time to time the head is uneasily moved, and the animal seems to react (by closing the eyes) to loud and sharp sounds—although my evidence on this point is not very clear.

In short, the decerebrate monkey appears to be in a state which closely resembles that of light sleep, and the fact that, in this condition, these slow and maintained postural activities of flexion and extension in the arm may occur after decerebration shews conclusively that they are conditioned by centres below those in the cerebrum.

IV. *Electrical Stimulation of Regions in the Cross-section of the Mid-brain Dorsal to the Area of the Cortico-spinal Tract.*

Unipolar stimulation of the cross-section of the mid-brain at the level of the anterior colliculi—when applied at a point in an area which lies dorsal to that of the cortico-spinal tract—gives a definite movement of the arms. The focal point in this area—that is, the most excitable point in it—lies ventral to the central canal. The area includes that of the nucleus ruber and of the posterior longitudinal bundle.

Stimulation within this area upon one side of the mid-brain is accompanied by the assumption of a definite posture on the part of the animal. The back of the head is twisted towards the same side and the face away from it, the neck is bent concave to the same side (sometimes the face seems to be turned to the same side). The arm of the same side is flexed, that of the opposite side is extended. The lower limb of the same side is extended and the opposite one flexed (but at one period in an experiment in which this was usually the case I observed the ipsilateral hind limb to be flexed and the contralateral to be extended). The tail is bent to the same side. I have not been able carefully to examine the movements of the trunk.

When stimulation has ceased the posture is maintained. Thus if the attention be directed to the movements of the arm muscles alone it is found that the ipsilateral flexion (or contralateral extension) may outlive the evoking stimulus for several minutes.

1. *The Ipsilateral Reaction.*—When the movements of individual muscles in the arm are examined (*e.g.* fig. 2) it is found that stimulation of the ipsilateral area is immediately followed by a sharp flexor contraction. This soon attains a maximum at which it persists throughout the application of the stimulus. If extensor tonus is in being the flexor contraction is accompanied by reciprocal extensor relaxation. Sometimes during a long application of the exciting stimulus an extensor contraction—accompanied by slow flexor relaxation—may appear late in the period of stimulation. On withdrawal of the stimulus there is usually no relaxation of the state of flexor contraction, which then may persist for many minutes. This is the typical reaction, and by far the most common. But flexor relaxation occasionally occurs at the termination of stimulation, and this may be followed by an extensor terminal contraction which is comparatively well maintained. All these types of reaction have been seen 10 months after the division of all the posterior spinal roots supplying the left arm.

2. *The Contralateral Reaction.*—The result of stimulation of the contralateral area is to evoke a contraction in the extensor muscle (*e.g.* fig. 4).

This is accompanied by reciprocal flexor relaxation if there is flexor tonus at the commencement of stimulation. The extensor contraction is a more slow movement than the flexor contraction in the ipsilateral reaction. Having attained a maximum this persists throughout the period of stimulation and is continued after termination of stimulation as extensor postural after-discharge. This is often as well maintained as the flexor after-discharge in the ipsilateral reaction, but sometimes it dies away more rapidly. Occasionally augmented extensor contraction may be seen, and it sometimes happens that the terminal phenomena consist of extensor relaxation and flexor rebound contraction. This is rare and has occurred when there was considerable flexor tonus in being at the time of application of the ipsilateral stimulus—although even in these circumstances extensor after-discharge is the more common. The flexor rebound has been observed to change to extensor after-discharge after mesial longitudinal section of the mid-brain. Good after-discharge may be seen in the " de-afferented " condition.

3. *The Synchronous Compounding of Ipsilateral and Contralateral Reactions.*—The two reactions may obviously be synchronously compounded in such a manner that the ipsilateral interrupts a contralateral " background " or the contralateral an ipsilateral " background."

When compounded against an ipsilateral " background " (flexion) the effect of stimulation of the contralateral area (extension) is to produce relaxation of the " background " flexor contraction. This may be complete or it may be incomplete. When the relaxation is not complete it is found that stronger contralateral stimulation produces greater flexor relaxation during double stimulation. The flexor relaxation may be accompanied by reciprocal extensor contraction—which is, however, not so great in extent as that in the " pure " contralateral reaction (fig. 1). On the other hand there may appear no extensor contraction during double stimulation—even when that is present in the " pure " contralateral reaction. Although the extensor contraction is a slow one the flexor relaxation is a very rapid movement, but the latency of flexor relaxation is usually great. When the interrupting contralateral stimulus is withdrawn and the ipsilateral stimulus is continued there occurs a restitution of flexor contraction. This is usually a rapid movement even where there is a good extensor after-discharge in the contralateral reaction. The restituted flexor contraction may attain a level as great as that at the corresponding point in a " pure " ipsilateral reaction (fig. 3, reaction " a "). Withdrawal of the ipsilateral " background " stimulus is followed by a flexor after-discharge just as in the " pure " reaction. In one instance an extensor terminal contraction and flexor terminal relaxation were seen. With the exception of the last phenomenon and of extensor

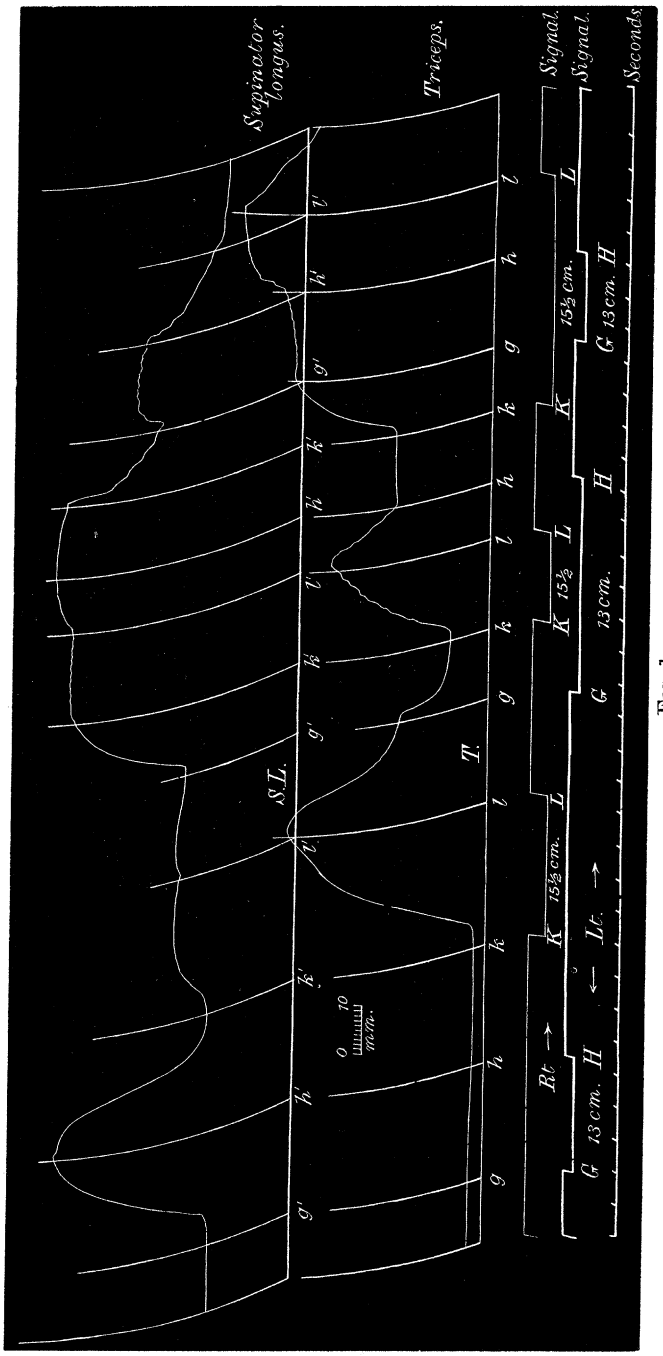

FIG. 1.

FIG. 1.—Experiment M, XXIX, record 327, 8860 ; 1.6.13.—*Macacus rhesus*. The record was obtained 1 hour after decerebration, and 12 minutes after mesial longitudinal

division of the mid-brain. The letters G–H (ordinates g, g'–h, h') denote the period of stimulation of the ipsilateral "dorsal focal point" (posterior longitudinal bundle ?) in the cross-section of the mid-brain at the anterior colliculi. The letters K–L (k, k'–l, l') in a similar manner denote contralateral stimulation. The upper record registers contraction (up) and relaxation (down) of the elbow flexor—supinator longus. The lower record registers similar movements of the elbow extensor—humeral head of triceps. Below these are the signal lines and a time tracing which registers seconds. A millimetre scale is reproduced, having been drawn upon the record before varnishing.

The first reaction is an ipsilateral one. On withdrawal of the stimulus the flexor after-discharge is extremely poor.

The second reaction is a contralateral one. Extensor contraction occurs. This is here accompanied by abnormal flexor contraction—not usually seen. There is an extensor after-discharge which is not well marked, but a sudden relaxation of this is seen at the commencement of the third reaction, which opens with the ipsilateral reaction.

In the third reaction the two stimuli are compounded synchronously with an ipsilateral "background." In the phase of double stimulation (k, k'–l, l') there is extensor contraction and a partial and slight flexor relaxation. In this phase small rhythmic irregularities are evident in the two records. These are related to a slowing and deepening of respiration which then occurred. It will be observed that the extensor contraction is less in extent than that of the "pure" contralateral reaction (the second reaction of the record). On withdrawal of the contralateral stimulus there occurs flexor restitution and extensor relaxation. Flexor after-discharge occurs on withdrawal of the ipsilateral "background" stimulus, and is much better sustained than that in the preceding "pure" ipsilateral reaction.

In the fourth reaction of the record the "background" is contralateral (extension). The contralateral stimulus is applied in the flexor after-discharge of the preceding reaction and causes flexor relaxation (at k, k'). During double stimulation (g, g'–h, h') there occurs a partial and slight extensor relaxation accompanied by reciprocal flexor contraction. Withdrawal of the ipsilateral stimulus is followed by flexor relaxation and extensor restitution of contraction. Withdrawal of the "background" contralateral stimulus is followed by extensor after-discharge.

This figure demonstrates the presence of flexor after-discharge in the ipsilateral reaction and extensor after-discharge in the contralateral; of the effects of compounding the two in temporal succession; and of the effects of synchronous compounding with ipsilateral and contralateral "backgrounds," all after mesial longitudinal division of the mid-brain.

contraction during double stimulation all these points have been observed in the "de-afferented" condition as well as in the "normal."

When compounded against a contralateral "background" (extension) an interrupting ipsilateral stimulus (flexion) evokes extensor relaxation and flexor contraction. Where the ipsilateral stimulus is comparatively weak the extensor relaxation may be incomplete (fig. 2). Where stronger it may be complete. Withdrawal of the interrupting ipsilateral stimulus is accompanied by a sharp relaxation of the flexor contraction. This may occur even when there is a flexor after-discharge in the ipsilateral reaction and when the contralateral "background" stimulus is ineffective. The flexor relaxation

when the contralateral stimulus is effective may yet not be accompanied by restitution of extensor contraction. But that restitution may occur (figs. 1, 2). It then is a slow movement and closely resembles the extensor contraction in the "pure" contralateral reaction. Sometimes the flexor relaxation on withdrawal of the interrupting ipsilateral stimulus is a slow one (figs. 1, 2). Occasionally the flexor contraction may even be sustained after withdrawal of the ipsilateral stimulus (fig. 3). In such cases the flexor contraction is

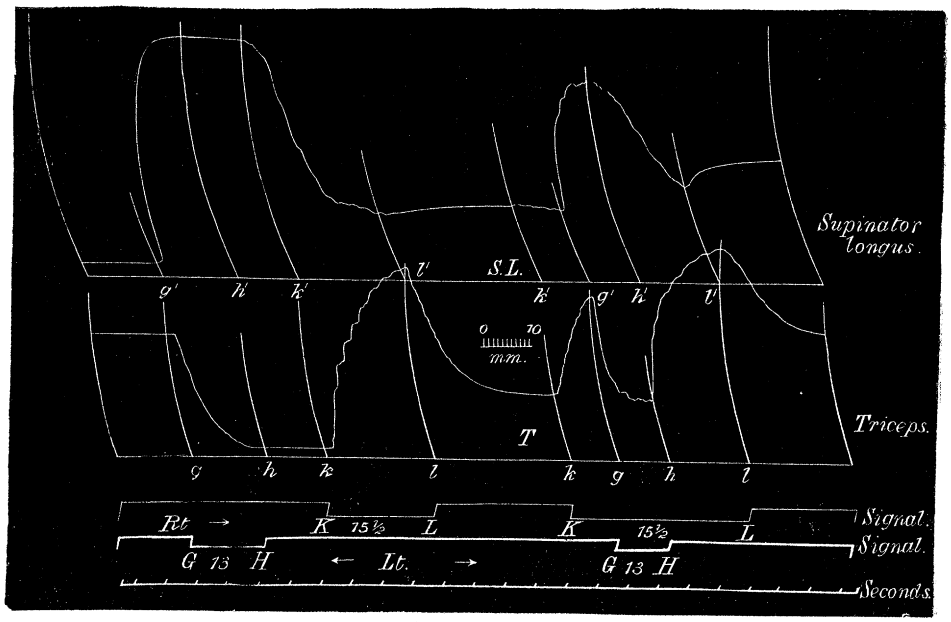

FIG. 2.—Experiment M, XXIX, record 327, 8855; 1.6.13.—*Macacus rhesus*. From the same experiment as fig. 1. This record was obtained 42 minutes after decerebration and *before* the mesial longitudinal division of the mid-brain.

The first reaction is here an ipsilateral one, and it is applied during the presence of an extensor tonus from a preceding contralateral reaction. On stimulation extensor relaxation and flexor contraction occur. The ipsilateral reaction is followed by a good flexor after-discharge.

The second reaction is a contralateral one. Here there occur flexor relaxation and extensor contraction. The extensor contraction is again rhythmically notched. The extensor after-discharge is not well marked.

The third reaction is compound. The contralateral stimulus is first applied, and is then interrupted by an ipsilateral. During double stimulation (g, g'–h, h') there is flexor contraction and extensor relaxation. The latter is not to so low a level, and the former is not to so high a level as those in the "pure" ipsilateral reaction. Withdrawal of the ipsilateral stimulus is followed by a slow flexor relaxation (it is usually more rapid) and by extensor restitution of contraction.

Compare this figure with fig. 1 (after mesial longitudinal division of the mid-brain). Here the effects of compounding the two reactions synchronously and in temporal succession are demonstrated as they occurred before the lesion.

not usually sustained on withdrawal of the contralateral "background" stimulus. Where extensor restitution of contraction occurs the withdrawal of the contralateral stimulus is followed by extensor after-discharge. In one

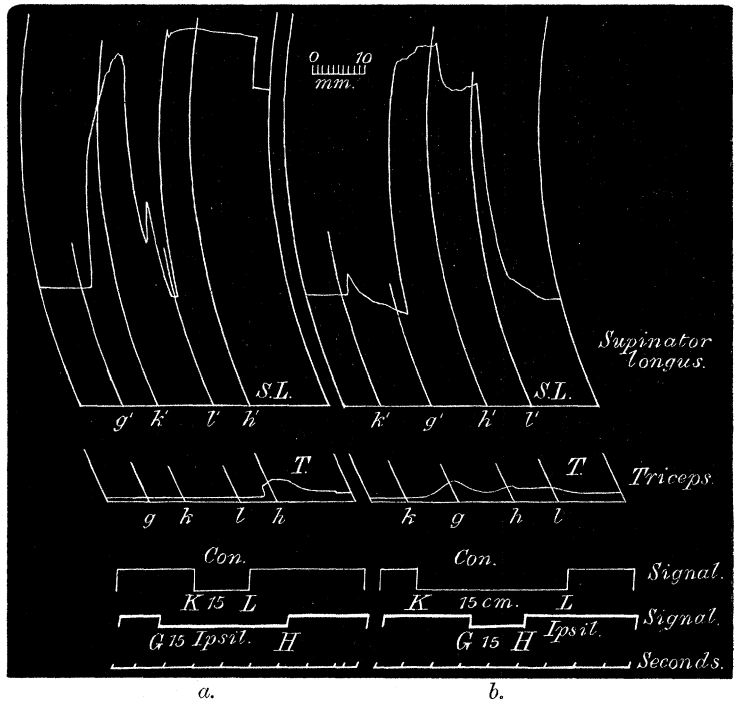

FIG. 3.—Experiment M, XXIV, record 311, 8362 ; 31.3.13.—*Macacus rhesus.* The dorsal spinal roots of the left (recording) fore limb divided in May, 1912. A reaction obtained 44 minutes after decerebration.

The first reaction (*a*) is a compound one with an ipsilateral "background." During double stimulation there is flexor relaxation, but no extensor contraction. The latency of the flexor relaxation is great. On withdrawal of the contralateral stimulus there is flexor restitution of contraction which occurs as a very sudden movement. On withdrawal of the ipsilateral "background" stimulus there is a marked flexor after-discharge. The sudden drop in the flexor after-discharge seen about 3 mm. before the final ordinate in reaction (*a*) occurred during a period of 15 seconds in which the kymograph was stopped—it therefore represents a very slow movement.

The second reaction (*b*) is a compound one in which the contralateral reaction is the "background." During double stimulation flexor contraction and extensor relaxation occur. But on withdrawal of the ipsilateral interrupting stimulus (at *h*, *h'*) there continues a flexor after-discharge. On withdrawal of the contralateral "background" stimulus this disappears.

case, where flexor relaxation occurred on withdrawal of the interrupting ipsilateral stimulus, there yet occurred flexor rebound on withdrawal of the contralateral "background" stimulus. There the same phenomenon occurred

in the "pure" contralateral reaction. With regard to the phenomena described in this paragraph there is little difference between the "de-afferented" and the "normal" conditions.

It therefore appears that the phenomena obtained when the two areas in the cross-section of the mid-brain are simultaneously stimulated closely resemble those obtained when the movements of two antagonists in response to peripheral nerve stimulation are examined. "Algebraic summation" seems to occur, and the phenomena which occur when the interrupting stimulus is withdrawn and the "background" still continued nearly approximate to those seen under similar conditions in the peripheral reflexes where the "pure" reactions are followed by good "after-discharge."

4. *The Compounding of Ipsilateral and Contralateral Reactions in Temporal Succession.*—Where the ipsilateral reaction is followed by flexor after-discharge and the contralateral by extensor after-discharge the two reactions may be compounded in such a manner that the one falls during the after-discharge of the other. If this is done the contralateral reaction (extension) at once produces a very sharp relaxation of the flexor after-discharge of the ipsilateral reaction. On withdrawal of the contralateral stimulus an extensor after-discharge is left in being, and this is at once reduced if the ipsilateral stimulus is repeated, and so on (fig. 2). If the contralateral stimulus is weak or of very short duration there may be incomplete relaxation of a flexor after-discharge. If the ipsilateral stimulus is weak there may be a partial relaxation of an extensor after-discharge, and this may thereafter be reconstituted.

5. *The Geographical Position of the "Focal Point."*—When stimulation applied to one or other side of the cross-section of the mid-brain gives one or other of these reactions it is usually found that the area from which they may be obtained is comparatively large. The minimal reaction may, however, be localised to a comparatively small area. This area ("focal point") lies about 3 to 4 mm. ventral to the dorsal surface of the mid-brain, and about 2 to 3 mm. from the mesial plane. The surrounding parts are inexcitable, except, perhaps, those immediately between the focal point and the mesial plane.

In one experiment in which decerebration was comparatively high—the division of the neuraxis passing just oral to the anterior colliculi—the focal point was found to be much more ventral than this, about 7–8 mm. from the dorsal surface. The ipsilateral reaction was of the usual type. The contralateral reaction gave relaxation of a flexor after-discharge (if that was in being) and extensor contraction, but on withdrawing the stimulus there was at once sharp extensor relaxation and a marked flexor rebound contraction. The mid-brain was then split in the mesial plane (the section was found to

have passed out of the mesial plane into the left half of the neuraxis at the level of the posterior colliculi). Immediately thereafter the focal point was found to be in the usual more dorsal position. Ipsilateral stimulation gave the usual reaction, and contralateral stimulation gave the same reaction as before, save that there was marked extensor after discharge and no flexor rebound contraction.

V. *The Effect of Various Lesions.*

1. *Mesial Section between the Right and Left Halves of the Mid-brain.*—When the reactions are obtained from the dorsal focal point there may be no change in them after this lesion. The phenomena during the immediate and successive compounding of the two reactions may be the same as before (figs. 1, 4). The excitability may be depressed slightly, or it may remain unchanged, or it may even appear to be raised. The effects of mesial section in a case where the lower focal point was effective have been described in the previous section.

2. *Right Semi-section of the Mid-brain between Anterior and Posterior Colliculi.*—After this lesion it is found that the ipsilateral reaction (from the left side of the mid-brain) is unimpaired, but the contralateral reaction (from the right side of the mid-brain above the level of the semi-section) is abolished. The contralateral reaction may at once be obtained by stimulation of the caudal surface of the cut in the mid-brain.

3. *Division of the Right Superior Cerebellar Peduncle.*—This was found to have no appreciable effect upon the reactions and their compound effects. The experiments upon the cerebellar peduncles, in view of the effects of removal of the whole cerebellum, were not continued.

4. *Complete Removal of the Cerebellum.*—In several experiments the cerebellum has been completely removed. After this lesion there is at first no change in the two reactions. Flexor after-discharge follows the ipsilateral reaction and extensor after-discharge the contralateral, and the effects of compounding the two in temporal succession is the usual one (fig. 5). This may last for 30 minutes or more. Thereafter the flexor after-discharge disappears, the withdrawal of the ipsilateral stimulus being followed by sharp flexor relaxation. In one experiment the extensor after-discharge still persisted. No change in the excitability of the reactions may occur. In other cases the flexor after-discharge may disappear from the moment of removal of the cerebellum (the reactions have usually been tested within one minute of that removal). In one case the contralateral reaction reversed to flexion with the same strength of stimulus which before the removal gave extension. The procedure of removal of the cerebellum has been observed

to be followed by marked extensor tonus. In one case marked flexor tonus was present immediately after the removal.

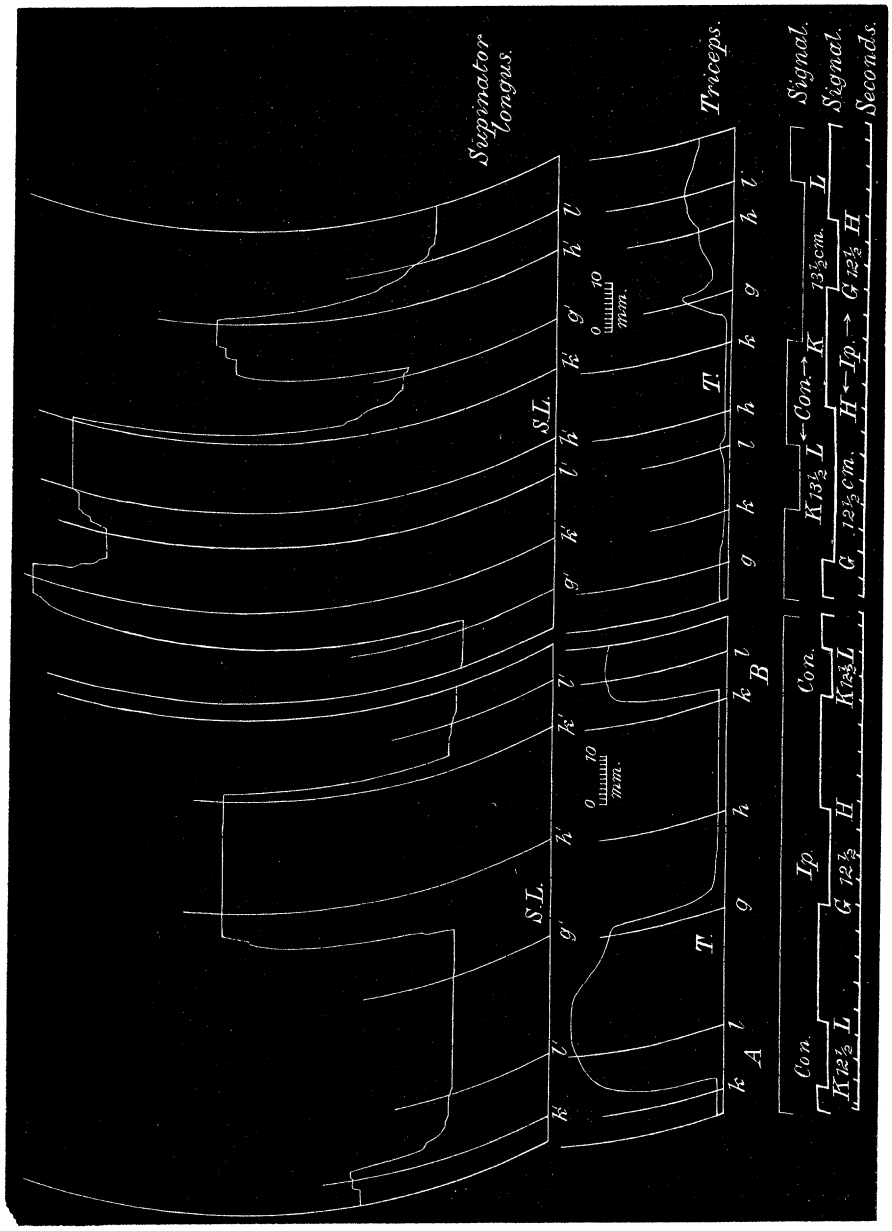

Fig. 4.—Experiment M, XXX, record 329, 8885 ; 6.6.13.—*Macacus rhesus*. The two reactions are obtained 50 minutes after decerebration, and 12 minutes after mesial longitudinal division of the mid-brain.

In *a* the first reaction is contralateral. Applied during a flexor after-discharge, it gives flexor relaxation and extensor contraction, and is itself followed by a marked extensor after-discharge. The second reaction is applied during this. It is an ipsilateral one, and gives extensor relaxation and flexor contraction, being followed by a well sustained flexor after-discharge. The third reaction is again contralateral, and repeats the phenomena in the first.

In *b* the two stimuli are synchronously compounded. In the first reaction the ipsilateral "background" shows but small relaxation during double stimulation. In the second the contralateral "background" is weak, and yet the flexor contraction of double stimulation is markedly smaller than that in the "pure" ipsilateral reaction.

This figure, and also fig. 1, demonstrates the antagonistic effects of the two stimuli after mesial longitudinal division of the mid-brain.

5. *Removal of Mid-brain.*—In one experiment in which flexor after-discharge in the ipsilateral reaction outlasted for some time the removal of the cerebellum it was found that it also outlasted removal of part of the

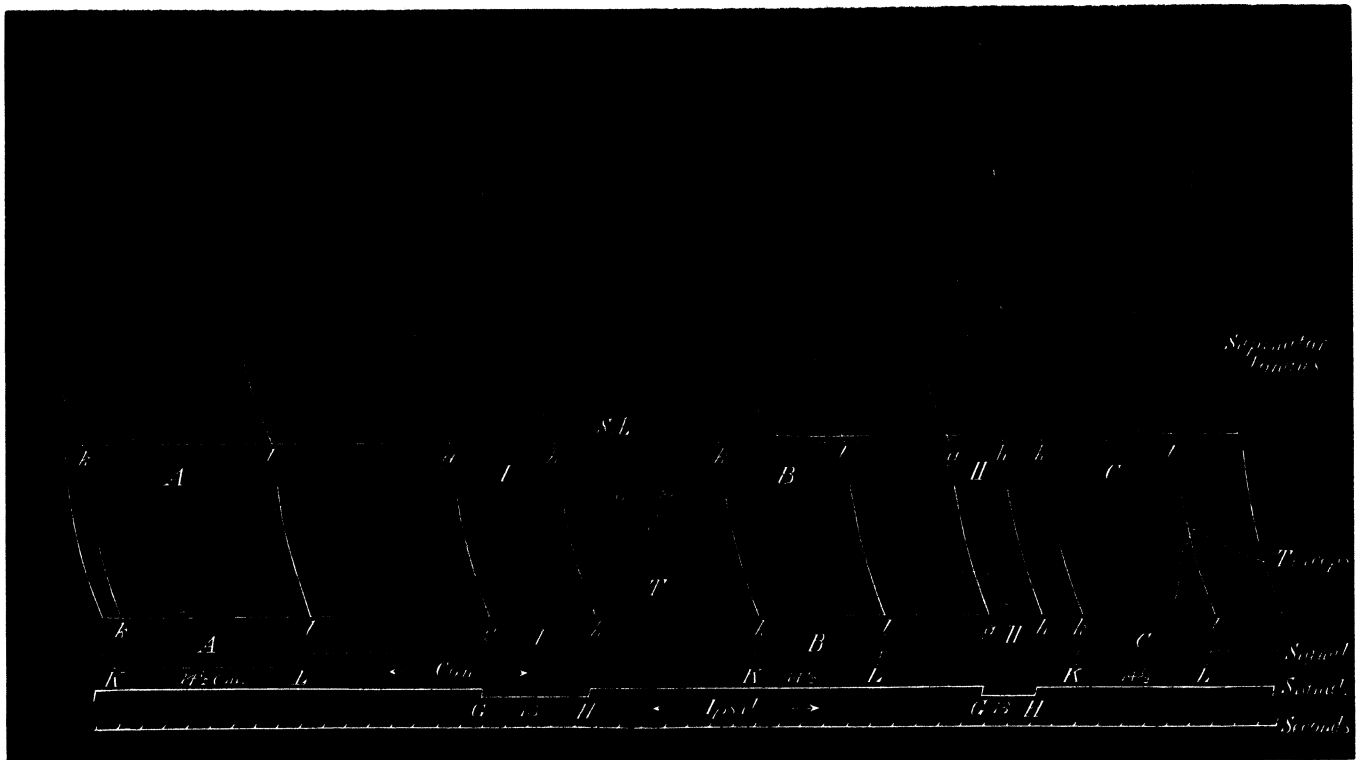

FIG. 5.—Experiment M, XXXV, record 337, 9094; 17.6.13.—*Callothrix.* The reactions are obtained 55 minutes after decerebration and 10 minutes after complete removal of the cerebellum.

Flexor tonus is in being at the commencement of the series. Reactions "A," "B," and "C" are contralateral. They demonstrate flexor relaxation and extensor contraction during double stimulation and extensor after-discharge after stimulation.

Reactions "I" and "II" are ipsilateral. During stimulation there is first relaxation of the extensor after-discharge contraction, and then flexor contraction. On cessation of stimulation there is a partial flexor relaxation which becomes arrested, and flexor contraction then persists as after-discharge.

This figure demonstrates—*after removal of the cerebellum*—(*a*) the persistence of flexor after-discharge in the ipsilateral reaction from the cross-section of the mid-brain, and the persistence of extensor after-discharge in the contralateral reaction; and (*b*) the persistence of the antagonistic effects of these two reactions when they are compounded in temporal succession.

mid-brain. The extensor contraction in the contralateral reaction had disappeared, but the ipsilateral reaction was untouched. The anterior colliculi were then first removed. Flexor after-discharge still occurred after the ipsilateral reaction. If the contralateral stimulus was applied during this flexor after-discharge there occurred flexor relaxation which continued after the cessation of the contralateral stimulus. When the posterior colliculi were then removed the flexor after-discharge in the ipsilateral reaction was not clearly marked, and the contralateral effect was not obtained (the contralateral reaction in response to weak stimuli appeared to be one of flexion). When the oral half of the pons Varolii was removed after a transverse section the reaction which accompanied stimulation of the ipsilateral area was not followed by any after-discharge. In another experiment the flexor after-discharge had disappeared from the ipsilateral reaction after removal of the cerebellum, and it remained absent after further removal of the mid-brain. Here also the contralateral reaction appeared to be one of flexion.

VI. *Electrical Stimulation of the Crus Cerebri.*

It may be suggested that the results above described might, in part at any rate, be due to stimulation of the crura cerebri by spread of current. That this is not the case is shewn by two observations.

Of these, the first is the fact that with the strength of stimuli used the ipsilateral crus cerebri is inexcitable as regards the movements of the arm of its own side of the body. The contralateral crus is excitable, but the movements of the elbow obtained from it are almost invariably flexion, whereas the contralateral reactions from the area in the cross-section of the mid-brain dorsal to it are those of extension. Further, there is an inexcitable field between the two.

The second observation is that the movements of flexion excited by stimulation of the contralateral crus are unlike those obtained on stimulation of the area in the ipsilateral side of the cross-section of the mid-brain. The crus flexion is almost always a slow one and "climbs" during the course of application of the stimulus, so that its maximum is almost always at the point of cessation of stimulation. Cessation of stimulation is followed by a very sudden relaxation, so that the arm "flops." This is extremely characteristic.

VII. *Compound Stimulation of Crus and the more Dorsal Excitable Area in the Cross-section of the Mid-brain.*

In these experiments the effects of compound stimulation of various kinds have been examined. Here there is not space to mention all of these, but

the phenomena when crus is pitted against the excitable area which lies more dorsally in the cross-section of the mid-brain are of great interest.

1. *Immediate Compounding of Crus against Contralateral Reaction (Extension).*—The crus reaction used was the typical contralateral flexion. In one experiment ("de-afferented"), where the "background" of the compound reaction was that of the contralateral reaction (extension with extensor after-discharge) the interrupting crus reaction caused extensor relaxation accompanied by flexor contraction of the typical crus type. Withdrawal of the crus stimulus gave flexor relaxation and reconstitution of extensor contraction. Withdrawal of the "background" contralateral area stimulus was followed by the usual extensor after-discharge. When the contralateral reaction is made to interrupt the crus reaction a relaxation of the flexor contraction has been observed during double stimulation.

2. *Immediate Compounding of Crus against Ipsilateral Reaction (Flexion).*—Here when the ipsilateral reaction serves as the "background" there occurs flexor augmentation of contraction when the interrupting crus stimulus is applied. On withdrawal of that stimulus again, the ipsilateral reaction still continuing, the flexor contraction remains augmented. The subsequent after-discharge of the flexor on withdrawal of the "background" ipsilateral reaction may remain at this level.

3. *Compounding in Temporal Succession.*—When the ipsilateral reaction from the more dorsal excitable area in the cross-section of the mid-brain gives a marked flexor after-discharge and the contralateral crus stimulus is then applied, augmentation of flexor contraction may occur. But, on withdrawal of the crus stimulus, there is immediate and very sudden flexor relaxation—exactly similar to that which follows a "pure" contralateral crus stimulus. This phenomenon is the more remarkable in that it may occur where the flexor after-discharge after the ipsilateral reaction is of great extent and very great duration. It seems to indicate that the flexor relaxation after crus stimulation is, as it were, a positive phenomenon (fig. 6). This phenomenon has been observed in the "de-afferented" condition. It has also been observed after removal of the cerebellum.

VIII. *Stimulation of other Points in the Mid-brain and Hind-brain.*

In passing, I should like to note some effects of the stimulation of other points in the hind-brain and mid-brain.

In one experiment, where the level of cross-section in decerebration was just above the anterior colliculi, a curious bilateral kick-like movement of the lower limbs was obtained on stimulation of a small area on either side of the cross-section. This was to the side and dorsal in position, and it is

possible that the reaction was a reflex in connection with the optical mechanism.

In several experiments it was found that unipolar stimulation applied to a certain area on the ventral surface of the exposed fourth ventricle evoked

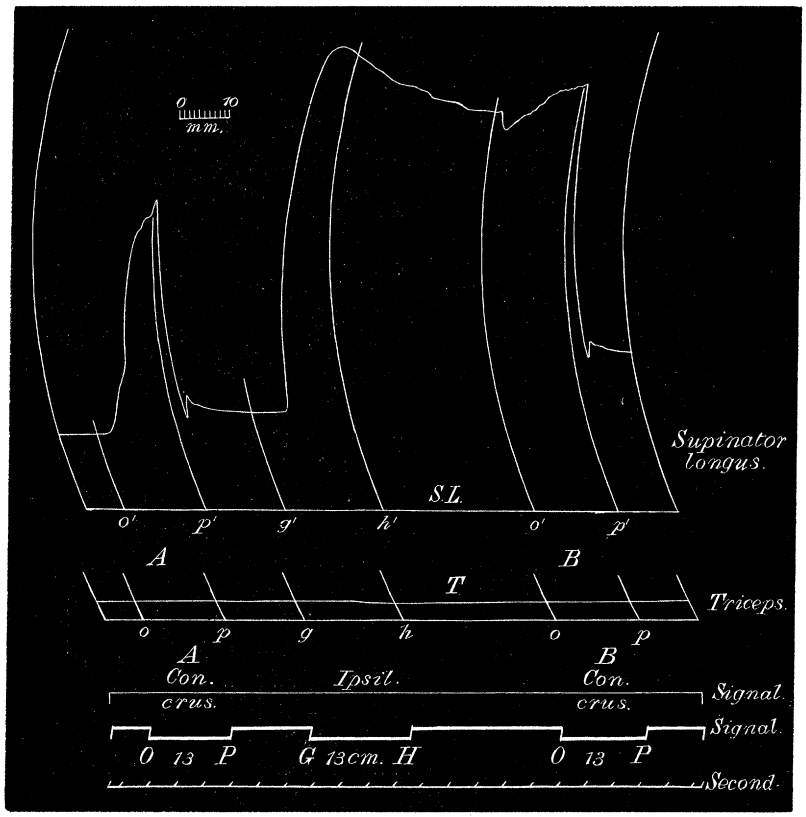

FIG. 6.—Experiment M, XXV, record 315, 8481; 1.4.13.—*Macacus rhesus*. All the dorsal spinal roots of the left (recording) fore limb divided in May, 1912. A record of the reactions from the ipsilateral area on the cross-section of the mid-brain and of the reactions from the contralateral crus cerebri obtained 1 hour and 8 minutes after decerebration.

The first reaction (O–P, ordinates *o*, *o'*–*p*, *p'*) is that from the contralateral crus cerebri (A). It demonstrates the typical "climbing" form of the contraction, and the sudden relaxation on withdrawal of the exciting stimulus. [It was not possible to induce an after-discharge by repeated stimuli in series.]

In the second reaction an ipsilateral "dorsal focal point" stimulus is applied, and gives the usual flexion followed by flexor after-discharge in this experiment that would last for several minutes if undisturbed.

In the third reaction (B) the crus stimulus is repeated during this after-discharge. It gives first a slight relaxation, and then an augmentation of flexor contraction. But, nevertheless, on withdrawal of the crus stimulus the sudden relaxation occurs as in the "pure" crus reaction. The flexor after-discharge is abolished.

flexion of the ipsilateral arm. This area lay about 3 mm. above the tip of the calamus and was near the mid-line. To stimuli of a strength which could evoke this, the surrounding regions were inert.

Stimulation of the nucleus cuneatus in the medulla oblongata gives flexion of the ipsilateral arm. Stimulation of the nucleus gracilis gives movements of the lower limbs. It has been found in some experiments that the flexion of the arm evoked by stimulation of the ipsilateral nucleus cuneatus is followed by marked flexor after-discharge. This may occur in response to very weak stimuli, and in these experiments the cerebellum had been removed. The after-discharge has been found to disappear after removal of all in front of the medulla oblongata, and after removal of the mid-brain alone.

IX. *Conclusions.*

The "dorsal focal point" in the cross-section of the mid-brain—the results of stimulation of which are here described—corresponds geographically with the cross-section of the posterior longitudinal bundle at that level. The "ventral focal point" (described for one experiment) corresponds geographically with the area of the nucleus ruber. The effective strength of stimulation of these areas is much greater than that necessary to evoke reactions from the motor nuclei or from the nucleus cuneatus.

In these circumstances there is a great risk of error due to spread of current. But the fact that the reaction from the dorsal focal point is abolished after lateral semi-section of the mid-brain behind the point stimulated, and that the reaction may still be obtained from the caudal surface of the semi-section, makes it extremely probable that the phenomena here described are conditioned by stimulation of the posterior longitudinal bundle. That they are apparently unchanged after mesial longitudinal division of the mid-brain helps to confirm this view. Is it possible that the stimulation of the "ventral focal point" is stimulation of the rubro-spinal tract? My evidence at present is quite insufficient to make this certain, but there are certain points of interest which may be noted. In the first place, the excitability of this point drops after mesial longitudinal division of the mid-brain, and this looks as if there was a decussation of the tract stimulated in the mid-brain itself. Another point which may be noted is that, whereas before this mesial longitudinal division the ipsilateral reaction of the ventral focal point was one of flexion, after that division it appeared to yield ipsilateral extension. As I have said, the evidence on this point is quite incomplete, but may the guess be hazarded that the crossed and uncrossed portions of the rubro-spinal tract subserve different functions?

To turn again to the dorsal focal point (posterior longitudinal bundle?),

some phenomena of interest are presented. Of these the first is the characteristic tendency of the reactions to be followed by after-discharge (contralateral, extension; ipsilateral, flexion). The reflexes evoked are essentially postural. This attribute disappears neither after mesial longitudinal division of the mid-brain nor immediately after complete removal of the cerebellum. Postural tonus of a perfect maintenance may be evoked in the absence of the cerebellum by appropriate stimulation of these tracts. It is possible that their activity is one of the chief factors in the great postural reflexes, and that the cerebellum plays upon them but is not itself the originator of the postural after-discharges. That the after-discharges do slowly disappear after removal of the cerebellum may be due either to shock or perhaps to the removal of a function of the cerebellum in maintaining the proper activity of these paths and centres.

The second point of interest is the mutual antagonism of the right and left dorsal focal points. This, seen either in immediate or successive compounding of the two, does not disappear either after mesial longitudinal division of the mid-brain or after complete removal of the cerebellum. The point of common antagonism is below the mid-brain, and it may be surmised that it lies at as low a level as that of the spinal centres.

A third point of interest is that the reactions—with their typical after-discharges—may occur many months after division of the dorsal spinal roots of the arm. That is to say, appropriate stimulation in the region of the mid-brain may evoke an extensor postural tonus or a flexor postural tonus. Sherrington has found that the "decerebrate rigidity" which occurs after removal of the cerebrum does not occur in a "de-afferented" limb, but the fact that a condition which at any rate very closely resembles this state may be evoked in such limbs seems to point to the conclusion that the absence of this postural tonus in the decerebrate "de-afferented" animal is due to the failure of the ascending impulses from the limb which normally play—however indirectly—upon these mechanisms of the mid-brain, and that the mechanisms themselves if properly activated are still able to induce the tonus.

One point more may be referred to—the activity of the cortico-spinal tract. The activity of the posterior longitudinal bundle (?) seems essentially to be postural. That of the cortico-spinal tract seems essentially to be non-postural. When the stimulus is stopped the reaction at once fails, and that with great suddenness. When the flexion reaction of the contralateral crus cerebri is pitted against the flexor after-discharge of the ipsilateral dorsal focal point (posterior longitudinal bundle ?) the phenomena are of great interest. There occurs during stimulation of the crus immediate augmentation of flexion, and

it might have been supposed that the flexor after-discharge remained unimpaired after withdrawal of the crus stimulus. But this is not the case. Immediate relaxation of flexor contraction occurs just as in a "pure" crus reaction. To this extent the crus flexion reaction seems to be antagonistic to the flexion reaction of the after-discharge in the dorsal focal point reaction. The non-postural cerebral activity seems to abolish the postural mid-brain activity and thus to leave, perhaps, a virgin field for any subsequent reaction.

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*Synthesis by Sunlight in Relationship to the Origin of Life. Synthesis of Formaldehyde from Carbon Dioxide and Water by Inorganic Colloids acting as Transformers of Light Energy.**

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(Received June 24, 1913.)

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At a discussion on the origin of life held by the joint sections of Zoology and Physiology of the British Association, at the Dundee Meeting, September, 1912, it was suggested by Moore that the first step towards the origin of life must have been the synthesis of organic matter from inorganic by the agency of inorganic colloids acting as transformers or catalysts for radiant solar energy. This suggestion was amplified and explained in a book written in November, 1912, by the same author.†

It is important to emphasise the point that in considering the origin of life in a world containing inorganic matter only, the nutrition of the first living structure on such a world must be carefully borne in mind. This observation is still true whether life is to be regarded as arising *de novo* on the planet, or as being borne there from some other planet as a germ from pre-existent life. No living organism such as a bacterium or mould which did not possess the power of transforming energy and of synthesising organic

* The cost of materials and apparatus for this research have in part been defrayed by a grant from the Government Grant Committee of the Royal Society, and in part by a donation from Mr. William Johnston, of Liverpool.

† Moore, 'The Origin and Nature of Life,' pp. 181–193, Home University Library. Williams and Norgate, London.