"Experiments on the Brain of Monkeys.—No. I." By DAVID FERRIER, M.A., M.D., M.R.C.P., Professor of Forensic Medicine, King's College, London. Communicated by Dr. J. B. SANDERSON, F.R.S.

The facts recorded in this paper are the results obtained by electrical stimulation of the brain of monkeys, after the method described by the author in the West Riding Lunatic Asylum Medical Reports, vol. iii, 1873. They formed part of a paper "On the Localization of Function in the Brain," read before the Royal Society on March 5, 1874*. This memoir also contained the results of other experiments on the brain of monkeys, chiefly relating to the effects of localized lesions of several parts of the hemispheres, with a view to determine the significance, as regards sensation and motion, of the phenomena caused by electrical irritation. These experiments are not here recorded, but are reserved for comparison with the results of a more extended reinvestigation of a similar nature, on which the author has been for some time engaged, and which will shortly be laid before the Society.

In order to avoid unnecessary detail, and in order to place the results together for the purposes of comparison, the animals experimented on are described, the dates of experiment given, and numbers assigned to them, so that they may all be brought into relation with each other :—

Experiments on Monkeys (Macaques).

I.	Left hemisphere	.....	June 14, 1873.
II.	Right ,,	.....	June 18, ,,
III.	Left ,,	.....	June 23, ,,
IV.	Left ,,	.....	June 25, ,,
V.	Left ,,	.....	June 27, ,,
VI.	Right ,,	.....	July 4, ,,
VII.	Left ,,	.....	July 16, ,,
VIII.	Left ,,	.....	July 22, ,,
IX.	Right ,,	.....	July 25, ,,
X.	Right ,,	.....	Aug. 1, ,,
XI.	Left ,,	.....	Aug. 8, ,,
XII.	Right ,,	.....	Aug. 23, ,,
XIII.	Right ,,	.....	Sept. 5, ,,

The circles marked on the woodcuts indicate the regions stimulation of which is followed by the same results. Several applications of the electrodes (which do not cover a larger diameter than a quarter of an inch) in or near the same region are necessary to mark off the area. To exactly define it is hardly possible, as the areas overlap each other, so that a complex set of movements may be caused by the conjoint stimula-

* See Proceedings, vol. xxii. p. 229.

tion of two centres which individually are capable of differentiation. This is particularly liable to occur if the currents are too strong. The areas drawn on the woodcuts are therefore more or less indefinite as to their boundaries. Their centres indicate more precisely the points of exact localization.

Besides describing the results of stimulation by reference to the figures, I have indicated the position of the electrodes, as far as possible, in relation to the individual convolutions, so that comparison may be made with those of the human brain.

For this reason the results are classified, and not related in the order in which they were obtained during the course of experiment.

Fig. 1.

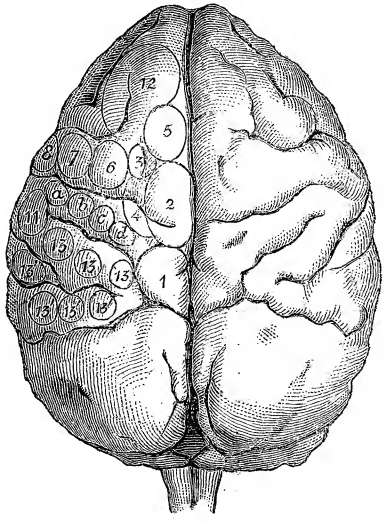
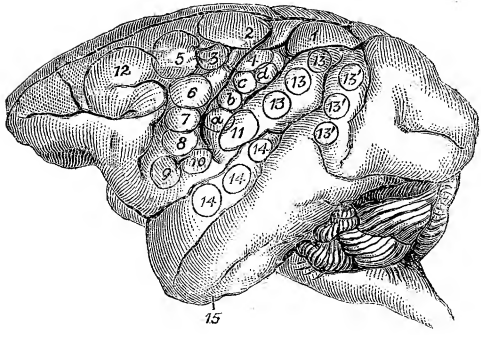


Fig. 2.



Circle (1), figs. 1 & 2, corresponding to the postero-parietal lobule, or superior extremity of the ascending parietal convolution. The region is embraced between the parieto-occipital fissure and a short perpendicular sulcus at right angles to the median fissure.

Results of stimulation :—

I. Not explored.

II. The left foot is flexed on the leg, and the toes are spread out and extended.

III. The right thigh is slightly flexed on the pelvis, the leg is extended, the foot flexed on the leg, and the toes are extended.

This result was obtained by stimulation of the posterior margin of the circle. At other points the advance of the whole limb was not so distinct, but the flexion of the foot and extension of the toes was very marked.

IV. The right leg is advanced, the foot flexed, and the toes extended.

In this case some movements of the arm were also made, but not of a constant nature, and were therefore regarded as accidental complications.

V. The right thigh is flexed on the pelvis, the leg extended, the foot flexed on the ankle, and the toes extended.

VI. Flexion of the left thigh on the pelvis, extension of the leg, flexion of the foot on the ankle, extension and spreading out of the toes.

VII. The right hind leg is advanced as in walking, the foot flexed on the ankle, and the toes extended.

In this case slight adduction of the foot was observed on stimulation, just posterior to the lower end of the short perpendicular sulcus already referred to.

VIII. Extension of the toes of the right foot, and flexion of the foot on the ankle.

In this case also a tendency to adduction of the leg and foot was observed.

IX. Flexion of left thigh on pelvis, extension of the toes, and flexion of the floot. (One observation only.)

X. Not explored.

XI. Extension of the toes of the right foot, and flexion of the foot on the ankle.

XII. Not explored.

XIII. Not explored.

The general result of stimulation of this region is to show that it is a centre for the movements of the hind leg, and apparently those concerned in walking.

It will be observed that in some cases the movement is only partially carried out. This is frequently the case, and, as will be seen in the subsequent details, a movement, at first of limited extent, gradually merges into a more complex one, involving numerous muscles.

Circle (2), figs. 1 & 2. This embraces the upper extremity of the ascending frontal convolution, and also stretches across the fissure of Rolando, so as to include the anterior division of the upper extremity of the ascending parietal convolution.

In the description reference is made to an anterior and posterior division, the boundary between the two being the fissure of Rolando. This is done because, though on analysis movements excited by stimulation of both are essentially the same, they are less distinctly brought out by stimulation of the posterior division alone, and are apt to merge into those resulting from excitation of circle (1).

Results of stimulation of the posterior division :—

I. Not explored.
II. Not explored.
III. Not explored.
IV. Not explored.
V. In this case there were movements of the right hind leg and foot, consisting in extension and then flexion and abduction of the thigh. Nothing more definite could be ascertained.
VI. In this case also there was first extension of the left thigh, then abduction or rotation outwards, while the foot was rotated inwards, the toes being extended and spread out.
VII. Not explored.
VIII. Rotation outwards of the right thigh, and rotation inwards of the leg and foot.
IX. Not explored.
X. Not explored.
XI. Similar to VIII.
XII. Not explored.
XIII. Not explored.

Results of stimulation of the anterior division (or upper part of the ascending frontal) :—

I. Not explored.
II. At first the left thigh was extended, and the leg and foot slightly rotated inwards, and then, on continuation of the electrization, the thigh was flexed on the pelvis and rotated outwards, while the leg and foot were rotated inwards, the toes being spread out in a

semiflexed condition, and pointing to the middle line of the body.

The combination of actions is just such as when a monkey scratches its abdomen with its hind leg.

The muscles of the trunk participated in the movements, so that the body was twisted to the opposite side.

III. The action in this case was in all respects similar to that recorded in II.

IV. In this case epileptic or choreic convulsions, which readily occurred on the slightest stimulation, rendered analysis of the movements impossible.

V. In this case the action described in II. was very distinct, viz. the rotation outwards of the thigh, the rotation inwards of the leg and foot, and the grasping portion of the toes pointing towards the middle line.

VI. As in I. and V., the thigh on the opposite side (left) was flexed and rotated outwards, the leg and foot inwards, while the toes were spread out.

VII. In this case also the movements were very distinct, consisting in rapid combined muscular action, bringing the foot and toes inward as if to scratch the body.

VIII. The results in all respects the same as VII.

IX. Similar action, viz. rotation outwards of the thigh, inwards of the leg, and the foot brought up with a sort of grasping movement of the toes to the middle line of the trunk.

X. Not explored.

XI. Action in all respects as described in IX.

XII. Not explored.

XIII. Not explored.

Circle (3), figs. 1 & 2, corresponding to the situation of a parallel sulcus in the upper part of the ascending frontal convolution.

It may be taken as included in the previous one, but is marked separately on account of being also a centre for the tail.

Results of stimulation:—

I. Twisting of the trunk to the left, along with some not well-defined movements of the right leg and tail.

II. In this case the same action was observed as resulting from stimulation of circle (2), viz. flexion of thigh, rotation outwards, leg and foot rotated inwards, with the toes stretched out, semiflexed towards the middle line of the body. Movement of the tail was not noted.

III. Similar action. Tail not noted.

IV. Not explored.

V. Similar action of the leg, but at the same time the right arm was retracted. (This action of the arm will receive explanation below.) The tail was not observed.

VI. Not explored.

VII. Movements of the right hind leg as before, and also of the tail. The movement of the tail was not noted as being of a definite character, nor whether it was moved to the right or left.

VIII. The same as VII.

IX. Also the same as VII.

X. Not explored.

XI. Gave the results described under VII.

XII. Not explored.

XIII. Not explored.

The general result of these observations, all agreeing with each other in essential respects, is to show that circle (2) is a centre for the hind leg of a different character from circle (1), being more concerned in the action of the hind leg as an organ of prehension or climbing, instead of being an organ of simple progression. The subdivision circle (3) seems to be a centre for the tail. As I have not had an opportunity of experimenting on monkeys with prehensile tails, I am unable to indicate further the special action of this centre in regard to it.

Circle (4), figs. 1 & 2, embracing a portion both of the ascending frontal and of the ascending parietal convolution, extending from the lower border of the parallel sulcus, already alluded to, to the anterior boundary of circle (1).

I. Not explored definitely.

II. The left humerus is adducted, the hand pronated, the whole arm straightened out and drawn backwards.

The action is such as is attributed to the latissimus dorsi, viz. a sort of swimming-action of the arm, with the palm of the hand directed backwards.

III. A similar extension and retraction backwards of the right arm.

IV. Retraction of the right arm, with the hand as already described.

V. Action as before of the latissimus dorsi, but at the same time also the right hind leg is acted on as if by stimulation of circle (1). In this case also the hand was firmly clenched.

Here it must be noted that the centres which cause the above-described movements of the hind leg, as well as those afterwards to be described which cause clenching of the fist, had been under stimulation previous to the exploration of this region. Hence the result is to be looked upon as the combined action of all three centres. This is the real difficulty experienced in analysis of the complex movements of the limbs, there being always a tendency to have complications arising from the irritable condition which continues in the regions which have been under experimentation. This, along with the tendency to convulsive spasms of a choreic or epileptiform nature, lasting for minutes after the cessation of stimulation, renders it frequently excessively difficult to draw accurate conclusions. The results described have always been those arrived at after as complete exclusion as possible of these adverse conditions.

VI. Retraction and straightening out of the left arm, as already described.

VII. Noted as action of the latissimus dorsi, this being regarded as the chief cause of the movement.

VIII. In this case the shoulder was first elevated, the humerus adducted, the wrist and hand fully extended, and the whole arm straightened and drawn backward in the manner already described in II.

IX. Left arm adducted, and then extended and retracted.

X. A similar result.

XI. Not explored.

XII. Not explored.

XIII. Action of the latissimus dorsi as already described. The condition of the hand is not noted.

The results of stimulation, therefore, of this region agree with each other.

I have observed frequently that only very partial action was occasionally obtained at some points in this circle; sometimes only an appearance of adduction of the arm. The complete action, however, appears to be such as I have described as resulting from stimulation of the centre of this circle.

Circle (5), figs. 1 & 2, corresponding to the posterior third of the superior frontal convolution.

I. The results in this case were not very definite. They consisted in a complication of the movements of the leg, already described as resulting from circle (2), along with an extension forwards of the right arm.

II. Here also extension forwards of the left arm and also of the leg. It is to be noted that the leg-centres had been already under stimulation previous to exploration of this centre.

III. Extension forwards of the right arm and hand.

IV. The results were not very definite, as the animal was continually being thrown into convulsive spasms on application of the electrodes.

V. The right arm and hand are extended forwards, as if to touch or reach something in front.

VI. Not explored.

VII. Rapid extension forwards of the whole right arm and hand.

VIII. Similar action.

IX. The left arm is outstretched, as if to touch some object in front.

X. Not explored.

XI. Similar result.

XII. Not explored.

XIII. Indefinite result, but apparently resembling IX.

Excluding complication due to conjoint irritation of the leg-centres, the results indicate a centre for a definite forward extension of the arm.

Ascending parietal convolution (*a*), (*b*), (*c*), (*d*), figs. 1 & 2. This is marked by the letters *a*, *b*, *c*, and *d*, indicating circles extending from the centre of the convolution to the fissure of Rolando and intra-parietal sulcus respectively.

Owing to the fact that many individual variations exist in the results obtained, they are detailed with more fulness in each case in the order of the experimentation, care being taken to compare accurately corresponding regions. The divergences are in a great measure to be explained by the fact that the movements caused involve the conjoint action of the flexor and extensor muscles of the wrist and fingers, and hence movements of an apparently opposite character seem to result from stimulation of the same point. A differentiation of centres for extension and centres for flexion could not be made out.

I. *a*. Flexion of the fingers of the right hand, abduction of the thumb, and slight rotation outwards of the wrist.

b. A similar action, but at the same time the humerus is adducted.

c. Similar to *b*.

d. Pronation of hand and flexion of the thumb and fingers.

Longer stimulation gave rise to clonic spasms of the wrist and fingers, continuing several seconds.

II. *d*. Sudden and quick extension of the wrist, and slightly of the fingers.

Continued in a choreic manner after stimulation.

c. Same result as *d.*

b. Extension of the fingers, but more especially of the thumb.

a. Thumb only is extended.

Spasmodic jerking of the thumb continued several seconds after withdrawal of the electrodes.

III. *a.* Clenching of the fist. The movement began with the thumb, which was first adducted.

b. As before, clenching of the fist; at the same time the extensors of the wrist and fingers were seen to be contracted.

c. Momentary application of the electrodes caused adduction of the thumb, followed on longer stimulation by clenching of the whole fist and slight pronation of the hand.

After several other regions had been explored, these points were again stimulated in succession.

The second result at point *d* was extension of the thumb and fingers instead of flexion.

A second stimulation of point *b* caused, first, adduction of all the fingers, then extension of the wrist and flexion of the distal phalanges, the proximal phalanges not being flexed till the wrist was fully extended.

The repeated application of the electrodes was followed in this animal by an epileptiform fit, affecting both sides of the body and lasting for three minutes.

IV. *a.* Abduction of the thumb.

At the same time the right angle of the mouth was retracted, owing, as will be seen, to the proximity of the centre for the platysma.

b. At first extension of the thumb, then, on longer irritation, extension of the wrist and flexion of the fingers.

c. Thumb adducted, and then firm clenching of the fist.

d. Clenching of the fist and pronation of the hand.

V. *a.* One application of the electrodes caused extension of the thumb; another caused adduction of the thumb and clenching of the fist, with extension of the wrist.

b. Clenching of the fist and extension of the wrist, as before.

c. Clenching of the fist as before, with complete pronation of the hand.

d. Clenching of the fist repeated, but complicated with the action of the latissimus dorsi and backward extension of the arm.

The reason of this is the proximity of the point *d* to circle (4).

VI. *a*, *b*, *c*, *d*. A similar result in all, viz. flexion of the fingers and extension of the carpus.

VII. *a.* Clenching of the fist.

The whole convolution was not explored, on account of constant repetition of choreic-like spasms.

VIII. *a.* Flexion of the fingers, passing into firm closure of the whole fist.

This action, slowly performed, began with the thumb, which became adducted, then the index-finger, the fingers in succession becoming adducted and then flexed till the fist became firmly closed.

b. Flexion and adduction of the thumb alone.

c. First adduction and flexion of the thumb, then firm closure of the fist and pronation of the arm.

IX. *a, b, c, d.* Slight touch causes adduction of the thumb, followed on longer stimulation by flexion of the fingers and complete closure of the fist.

Stimulation close to the fissure of Rolando caused the same movements, and also very decided extension of the wrist when the fist was completely closed.

X. Not explored.

XI. Results essentially similar to IX.

XII. Not explored.

XIII. Clenching of the fist as in former experiments.

The variations described in the movements resulting from stimulation of the ascending parietal convolution are apparently all referable to different aspects of combined muscular contractions, which in their completest action serve to cause closure of the fist or the grasping-action of the hand. Centres for the extensors and flexors, or for the flexors and extensors, of the individual digits could not be definitely made out.

Owing to the proximity of the centre for the platysma (circle (11)) at the lower end of the ascending parietal, very frequently, along with firm closure of the fist, there was decided retraction of the angle of the mouth on the same side.

Ascending frontal convolution :—

Circle (6), figs. 1 & 2. The position of this is on a level with the posterior extremity of the middle frontal convolution.

I. Supination of the hand and flexion of the forearm on the humerus, the hand being also more or less clenched. The action is such as may be attributed to the biceps, along with action of the flexors of the fingers.

Long-continued stimulation brings the hand up to the mouth, and at the same time the angle of the mouth is retracted and elevated.

This action of the mouth will be explained by reference to the action of the centre immediately below it.

II. Supination and flexion of the forearm and hand.

III. A similar result.

IV. Flexion of the forearm, clenching and supination of the hand.

V. Shoulder raised, forearm firmly flexed, hand clenched and supinated. The hand ultimately raised to the mouth, the angle of which is retracted and elevated.

VI. Flexion, with slight supination, of the forearm and hand.

VII. Flexion and supination of the right forearm and hand, accompanied with clenching of the fist when the stimulation was applied near the fissure of Rolando.

VIII. Apparent action of the biceps as before.

IX. Flexion and supination of the forearm and hand.

In this case it was found very decidedly that stimulation close to the fissure-of-Rolando side of the convolution caused the action of the biceps to be associated with clenching of the fist. Towards the lower margin of the circle the same movements were associated with retraction of the angle of the mouth.

X. Not explored.

XI. Same results as IX. exactly.

XII. Not explored.

XIII. Results as in other cases, viz. flexion and supination of forearm and hand, with clenching of the fist.

These uniform results point very clearly to this as the centre for the biceps and muscles concerned in bringing the hand up to the mouth.

Circle (7), figs. 1 & 2. Still in the ascending frontal convolution, in position immediately below the centre for the biceps.

I. Retraction and elevation of the right angle of the mouth.

II. Retraction (with elevation) of left angle of the mouth. Occasionally in stimulation the action was conjoined with that of the biceps.

III. Not explored.

IV. Not explored.

V. Spasm of the right angle of the mouth and of the cheek-pouch.

VI. Not explored.

VII. Elevation of right angle of mouth.

VIII. Same result as VII.

IX. Angle of the mouth raised and retracted, along with action of the biceps and flexors of the fingers.

X. A similar result. In this case, after several other parts had been under exploration, excitation of this region gave rise to a species

of epileptic fit, beginning in the left angle of the mouth, next proceeding to the left arm and hand, and, lastly, affecting the left leg and tail. The spasms next attacked the right angle of the mouth, the right arm, and the right leg in succession.

The fit lasted several minutes. The pupils were not dilated, nor did the animal apparently lose consciousness completely.

XI. Previous results confirmed.

XII. Not explored.

XIII. Contraction of left angle of mouth.

These results indicate that this is a centre for the muscles acting on the angle of the mouth, and apparently of the zygomatics.

Circle (8), figs. 1 & 2. Lower down in the same ascending frontal convolution.

I. The action is similar to that resulting from stimulation of the former centre, but seems especially to cause elevation of the lip and ala of the nose on the right side.

II. At the anterior part of the circle the left angle of the mouth is drawn upwards and backwards (zygomatici). At the posterior and lower margin of the circle the action is combined with that of the depressor anguli oris, so as to expose the canine teeth.

III. Not explored.

IV. Not explored.

V. Elevation of the upper lip (right side) and right side of nose.

Stimulation was followed by prolonged choreic-like twitching of the right angle of the mouth and ala of nose.

VI. Not explored.

VII. Elevation of right side of upper lip and ala of nose, along with depression of the lower lip.

VIII. Combined action of the elevator of the upper lip and ala of the nose and of the depressor anguli iris, so as to expose the canine teeth.

IX. Elevation of the upper lip and depression of the lower, so as to cause divergence of the lips and expose the teeth.

X. A similar result, but not so distinct, as the occurrence of choreic spasms interfered with successful observation.

XI. Results as in IX.

XII. Not explored.

XIII. At lower part of circle the depressor anguli oris is thrown into action; at the upper part the angle of the mouth is elevated.

These results are sufficiently uniform to indicate a centre for the facial muscles concerned in the production of that expressional action so fre-

quently exhibited by monkeys under the influence of fear or anger, viz. the exposure of the canine teeth.

Circles (9) and (10), fig. 2, corresponding in situation to the lower part of the ascending frontal convolution, or posterior part of the inferior frontal convolution, above the lower end of the fissure of Sylvius (Broca's convolution).

I. (9). The lips pout, mouth gradually opens, and the tongue is protruded.

(10). Action similar as to the mouth, but the tongue is retracted. Longer stimulation caused movements of the mouth and tongue, as in mastication.

II. (9). Mouth opened and tongue protruded.

(10). Tongue retracted.

Movements of mastication made by continued stimulation.

III. Same results as in I. and II.

IV. Not explored.

V. (9), as in former cases, causes opening of the mouth and protrusion of the tongue.

(10) causes retraction of the tongue.

Movements of mastication also caused on longer stimulation.

VI. Not explored.

VII. (9). Mouth opened and tongue protruded.

(10). Same result, but tongue apparently retracted.

VIII. (9). Opening of the mouth and protrusion of the tongue.

(10). Same result, with retraction of the tongue, followed on continuous stimulation with opening and shutting of the mouth, and alternate protrusion and retraction of the tongue.

IX. Similar results to VIII.

X. Not explored.

XI. Results of VIII. confirmed.

XII. Not explored.

XIII. Movements of the mouth and tongue, but not of any very definite character, the animal being in a state of exhaustion, and the excitability of the brain very weak.

These results point very definitely to a centre for the movements of the mouth and tongue, the muscles concerned in mastication and also in articulation. Its position is significant, as being the homologue in man of that region which is the seat of lesion in the disease known as aphasia, described as the posterior extremity of the lower frontal convolution. (In aphasia the lesion is generally on the left side, but the bilateral movements are seen by the experiments to be induced from both right and left sides.)

Circle (11), figs. 1 & 2, corresponding to the lower termination of the ascending parietal convolution and region of the inferior termination of the intraparietal sulcus (the conjoint extremities of the ascending parietal and angular gyrus).

I. Retraction of the right angle of the mouth, apparently the platysma thrown into action.

The effect was kept up after stimulation in a spasmodic manner.

II. Not explored.

III. Right angle of the mouth retracted. The head becomes drawn to the right by powerful contraction of the platysma.

IV. Not explored.

V. Retraction of the right angle of the mouth.

VI. Not explored.

VII. Not explored.

VIII. Retraction, with some appearance of elevation of the right angle of the mouth, along with powerful contraction of the subcutaneous muscles on the right side of the neck, evidently the platysma.

IX. Retraction of the left angle of the mouth. In this case the mouth was partially opened so as to expose the teeth.

X. Retraction of the left angle of the mouth.

This point was explored after several other regions had been under stimulation. The application of the electrodes to this point gave rise to spasms of a choreic or epileptiform nature, beginning in the left angle of the mouth, then affecting the left hand and arm, and lastly the left leg and tail. The choreic spasms then passed to the right angle of the mouth, the right hand and arm, and in a slight degree to the right leg and tail.

The fit lasted one or two minutes. It had not all the characters of a fully pronounced epileptic attack.

XI. Retraction of the right angle of the mouth. Recorded as action of the platysma.

XII. Not explored.

XIII. Strong contraction of the platysma, and retraction of the left angle of the mouth.

The results of stimulation of this centre agree with each other, and indicate a centre for the platysma. The frequent retraction of the angle of the mouth observed on causing clenching of the fist is explained by the proximity of the two centres to each other.

Island of Reil (central lobe), within fissure of Sylvius :—

Owing to the central lobe in the monkey being completely concealed within the lips of the fissure of Sylvius, mechanical injury and considerable hæmorrhage is necessarily caused in the attempt to expose it clearly. This is mentioned as a possible explanation of the negative results, but it is not sufficient to account for the apparent non-excitability of this region.

The island was exposed and experimented on in monkeys IX. and XIII.

IX. Electrization of the island of Reil gave no results.

Some movements of the mouth were caused during the introduction of the electrodes within the fissure, but were referred to stimulation of the mouth-centres in close proximity.

XIII. The result in this case was also negative.

To test this matter more fully, another monkey, not among those already numbered, was experimented on on December 10.

The lips of the fissure of Sylvius were carefully separated, without causing much injury or hæmorrhage. After the hæmorrhage had entirely ceased, the electrodes were applied directly to the surface of the central lobe.

No effect was observed.

After the animal had been allowed to rest for some time, it was then tested as to the excitability of the other centres. The hand, leg, and mouth could as usual be acted on by stimulation of their respective centres.

The electrodes, insulated up to the point, were again applied to the island of Reil.

No result was observed.

Stronger and continuous stimulation gave rise to choreic spasms of the angle of the mouth. This was attributed to diffusion of the current, owing to its being strengthened, and irritation of the proximate centres for the angle of the mouth.

Another application of the electrodes within the lower end of the fissure caused movements of the mouth and tongue. These also may have been due to conduction to the mouth-centres already described.

Beyond these, stimulation of the island of Reil yields negative results.

Circle (12), figs. 1 & 2, including the superior and middle frontal convolution from the antero-parietal sulcus (Huxley), sulcus præcentralis (Ecker), to the anterior extremity of the supero-frontal sulcus.

The results of stimulation of these convolutions were always so uniform, that the general result of experimentation in ten monkeys may be stated together. The results were :—

Elevation of the eyebrows and the upper eyelids, turning of the eyes and head to the opposite side, and great dilatation of both pupils.

Occasionally on stimulation of the centre for the forward extension of the hand this movement of the eyes and head was called into play.

Inferior frontal convolution (including all in advance of the sulcus præcentralis).

Stimulation of this region gave no results.

Antero-frontal region (including all in advance of the anterior extremity of the supero-frontal sulcus, and indicated sometimes by a slight sulcus at right angles to the median fissure) and orbital convolution.

These regions were subjected to stimulation in four cases, viz. I., V., VIII., and IX.

No results could be observed, either from the antero-frontal or orbital regions.

In a later experiment (December 2) on another monkey it was found that stimulation of the frontal part of the brain caused the eyes to move to the opposite side. This was found to be the case with irritation of both right and left hemispheres. The eyelids were not always opened, however, nor was dilatation of the pupils observed. Sometimes also the eyes moved upwards, instead of to the opposite side.

Irritation, therefore, of this region gives nothing definite as to their function.

Angular gyrus (*pli courbe*, Gratiolet).

Circle (13) and (13′), figs. 1 & 2. This is referred to as being composed of an ascending or anterior and a descending or posterior limb.

Results of stimulation :—

Ascending limb, circle (13).

I. Eyes directed upwards and to the right. Some oscillation of the right eyeball continued after the withdrawal of the electrodes.

On longer-continued stimulation the head is turned to the right, and the eyeballs to the right and slightly upwards.

II. Not explored.

III. Eyes directed upwards.
IV. Not explored.
V. Not explored.
VI. Not explored.
VII. Both eyes are directed to the right (whether there was any upward direction was not noted).
The pupils became contracted.
VIII. The eyes were directed to the right (notes do not mention as to whether any upward direction was observed). The pupil was thought to be slightly contracted. The eyelids during the stimulation had a tendency to close. The head also inclined to the right side.
IX. Both eyes directed upwards and to the left. Pupils contracted?
In this animal, which was allowed to remain quite conscious during stimulation, an experiment was made as to vision by holding before it a teaspoonful of milk, which it was eager to seize. In its attempt this point was stimulated, with the effect of causing confusion of vision and some difficulty in reaching the milk.
X. Both eyes turned to the left and slightly upwards. The pupils contract and the eyelids tend to close.
XI. Both eyes to the right and upwards. Pupils not observed.
XII. Both eyes to the left and upwards.
XIII. Both eyes to the left and upwards. The pupils contract.

Descending limb, circle (13′).

I. Eyes to the right and downwards. Head is inclined to the right side.
II., IV., V., VI. Not explored.
III. Eyes to the right and downwards.
VII. Both eyes directed to the right. Pupils contract.
VIII. Eyes down and to the right. Eyelids tend to close. Head directed slightly to the right side.
IX. Eyes directed down and to the left.
X. Eyes to the left and slightly downwards. The eyes half closed. Pupils contract.
XI. Eyes to the right and downwards. Pupils not observed.
XII. Same as XI.
XIII. Both eyes directed downwards and to the left. The pupils contracted.

These results are obtained on the *pli courbe* from the centre for the platysma (circle (11)) down to the termination of the descending limb in the *pli de passage* connecting it with the occipital lobe.

Experiments will be given subsequently as to the effects of destruction

of this region, and an attempt made to interpret the signification of these movements of the eyeballs.

Superior temporo-sphenoidal convolution, circles (14), fig. 2 (extending for about two thirds of its length from above downwards).

The results are only completely described after VII., as the ear was not particularly observed in the experiments going before. Results:—

I. Eyes opened and head turned to the right. Nothing observed as to the state of the pupils or ear.
II. Eyes open; eyeballs directed to the left, pupils dilate.
III. Eyes to the right, pupils dilate.
IV. Head and eyes quickly turn to the right. Pupils not observed.
V. Not explored.
VI. Not explored.
VII. Retraction (pricking) of the right ear, eyes widely opened, pupils dilated, and head and eyes turned rapidly to the right.
VIII. Retraction of right ear, head to the right, eyelids opened widely, eyes directed to the right with great dilatation of the pupils.
IX. Retraction of left ear, eyes opened widely, head quickly turned to the left. Pupils not observed.
X. Retraction of left ear, head and eyes turned to the left, and dilatation of the pupils.
XI. Retraction of right ear, eyes and head turned to the right, with dilatation of the pupils.
XII. A precisely similar result on left side.
XIII. Exactly same as XII.

The uniformity in the later experiments is complete. The results obtained are always quick and decided; they seem a combination of pricking of the ear, along with the effects described as resulting from stimulation of the frontal regions (circle (12)). Their significance will be alluded to subsequently.

The lower extremity of the same temporo-sphenoidal convolution gave no results in any of the animals in which this region was experimented on, viz. I., V., VIII., IX., X., and XIII.

Middle temporo-sphenoidal convolution (from the *pli de passage* downwards).

Nothing very definite was arrived at. In some the results were altogether negative; in others the following phenomena were noted, perhaps not altogether satisfactory as to their nature.

IX. On irritation of the lower end of the temporo-sphenoidal, just anterior to the lower temporo-sphenoidal convolution, a pursing

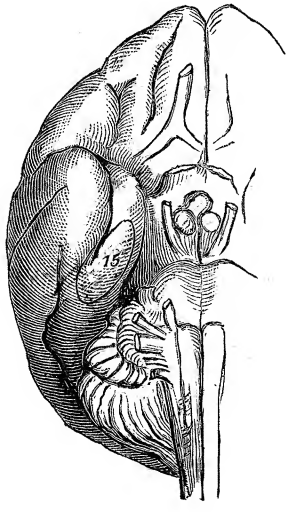
of the mouth, with some movements of the cheek-pouches and tongue, were observed.

X. In this case stimulation of the corresponding region caused some indistinct movements of the mouth and lips.

XIII. In this case there were some movements of the jaws; not of any decided character.

These are all the facts I have been able to gather from experimentation on this region, which is attended with some difficulty.

Fig. 3.



Lower temporo-sphenoidal convolution (inner aspect) and region of the uncinate convolution and occipito-temporal gyrus. Circle (15), figs. 2 & 3.

This region was reached and stimulated in the following cases with these results:—

VIII. Spasmodic contraction of the left lip and ala of the nose. The result was a sort of torsion or closure of the nostril, as when an irritant is applied to it. The action was on the same side, not crossed, as usual.

IX. Spasmodic torsion of the right lip and nostril, also on same side as stimulation.

X. Similar results, viz. an elevation of the right nostril and lip, so as to cause partial closure. In this case the phenomenon was observed on both sides, the right more especially, however.

XIII. Torsion of the right lip and nostril, as before.

In all these cases the phenomena were exactly alike. The fact of

their being on the same side as the stimulation, is explained by the origin of the olfactory tract from the *subiculum cornu ammonis*, and which passes on to the olfactory bulb without decussation.

The results plainly indicate a perception or subjective sensation of odours, and point to this as the central seat of the sense of smell.

Occipital lobes (superior and middle convolutions).

These were experimented on in I., III., V., VII., VIII., IX., X., XI., and XII.; also in another, not numbered, on November 21.

The results, except in the case of X., to be afterwards mentioned, were altogether negative as far as outward phenomena were concerned.

The negative results are not to be attributed to exhaustion of the excitability of the brain, for the other centres at the same time gave the usual results.

In the case of X. it was observed that stimulation of the inferior occipital convolution towards its inner aspect caused uneasy movements in the hind legs and tail, the head being turned to the left (opposite side) and backwards. Occasionally also a plaintive cry, as if from annoyance, was uttered. On cessation of the irritation the animal subsided into its dozing state.

Possibly the result may be attributed to conduction of the current to the tentorium or other part of the dura mater; but, owing to the difficulty of reaching this part of the brain, it is not easy to avoid all sources of fallacy.

Marginal convolution.

In the case of IX., the only one explored, it was found that irritation of the median aspects of the frontal and parietal convolutions caused movements of the head and limbs similar to those caused by stimulation of the centres on the outer aspect of the hemisphere.

Gyrus fornicatus.

No results were made out on slipping the electrodes deeply between the hemispheres.

Corpus callosum.

Stimulation of this was likewise unattended by any outward result.

These complete the regions which I have as yet been able to succeed in experimenting on.

I now pass from experiments on the hemispheres to similar experiments on the basal ganglia. These were reached in a few cases by division of the corpus callosum, turning out the hemisphere partially, and thus laying open the interior of the lateral ventricle.

Corpus striatum.

The corpus striatum was laid bare and stimulated in VIII. and XIII.

Results :—

VIII. Left corpus striatum.

Stimulation caused bending of the body to the right (pleurosthotonus) and rigidity of the limbs in the position of flexion.

XIII. Right corpus striatum.

Curving of the head and trunk to the left, the platysma being strongly in action, while the limbs were maintained in a rigid condition in the position of flexion.

The results indicated that all the muscles were simultaneously in action, individually stimulated by irritation of the cortical centres.

Optic thalamus.

Stimulated in VIII. and XIII. Results :—

IX. Entirely negative.

XIII. Also negative after several explorations of the upper surface.

Application of the electrodes to the inner aspect in the region of the soft commissure caused a spasmodic extension of the limbs. There was no cry of pain. The result was not constant, and it may therefore have been an accidental complication.

No other experiments were made on these ganglia in the monkey, on account of their resemblance to the results obtained on other animals.

Corpora quadrigemina.

These ganglia were subjected to experimentation in the following seven cases, viz. V., VI., VIII., IX., X., XII., XIII., with the results:—

V. In this case the exploration was not sufficiently definite, as the exact position of the electrodes was not observed, and death occurred before a more careful exploration could be made.

The application of the electrodes to the ganglia on the left side (position as to the testes or nates not ascertained) caused the animal to utter various barking, howling, or screaming sounds of an incongruous character.

The head was drawn back and to the right, and the right angle of the mouth was strongly retracted while the stimulation was kept up. The tail was raised and the limbs were thrown into contortions, but nothing further was ascertained, as the animal died from hæmorrhage.

VI. In this case irritation of the right anterior tubercle (nates) caused intense dilatation of both pupils (especially beginning in the left), elevation of the eyebrows, and turning of the eyeballs upwards and to the left, at the same time that the head was turned in the same direction with an intensely pathetic expression.

Momentary application of the electrodes to the posterior tubercles (testes) caused the animal to bark loudly, the sound passing with longer stimulation into every conceivable variation of howling and screaming.

Continuous application of the electrodes for several seconds caused ultimately firm clenching of the jaws, retraction of the angles of the mouth (particularly the left), elevation of the eyebrows, and retraction of the ears. The pupils were dilated, eyes widely open, and the head thrown back. The tail became elevated, the limbs, after contortions of various kinds, became rigidly drawn back, the arms drawn back and flexed at the elbows and closely approximated to the sides. A complete state of opisthotonus was induced. The dilatation of the pupils occurred on irritation of both nates and testes; the screaming &c. only on irritation of the testes.

VIII. The results in this case were essentially the same as in VI., as regards the dilatation of the pupils, howling, and rigidity of the limbs, &c.

IX. As before, stimulation of the anterior tubercle on the right side caused elevation of the eyebrows, dilatation of the pupils, and turning up of the eyes to the left. Irritation of the ganglia for some time caused a condition of opisthotonus, and the phenomena described under VI.

Irritation of the testes caused utterance of every variety of barking and howling, ultimately trismus and general opisthotonus.

X. Exactly as in IX.

XII. As before, irritation of the testes caused barking and howling.

When the animal was nearly dead irritation of the testes caused only powerful retraction of the angles of the mouth, so as to show the firmly clenched teeth.

XIII. In this case the results as to the nates and testes were in every respect similar to those already detailed in the former cases.

Cerebellum.

Experiments were also made on the cerebellum in five monkeys, some of those already alluded to, as well as others. Further than stating that the results which I have already described (West-Riding Reports) in the case of rabbits, viz. alteration of the optic axis in different directions according to the part stimulated, are confirmed in the case of monkeys, I do not at present intend entering into fuller details, but reserve a full consideration of this subject for a future paper.

There is great difficulty in ascertaining the exact causation and relation of the phenomena which are manifested on irritation of the cerebellum along with movements of the eyeballs. Among others, it may be stated, are certain movements of the limbs and trunk, which I interpret as indications of an attempt to adjust the equilibrium of the body in harmony with the ocular movements. On this point, however, further experiments are necessary.

An attempt to analyze and interpret the significance of these results will be made in the next communication.

Fig. 1.

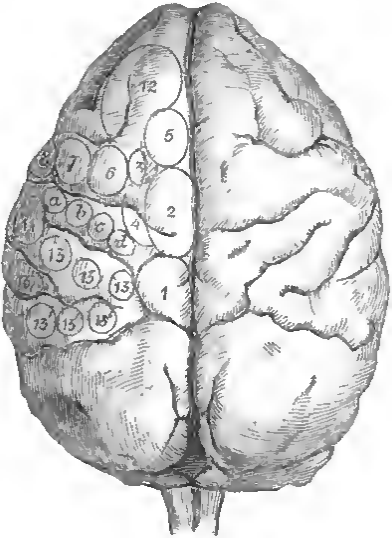


Fig. 2.

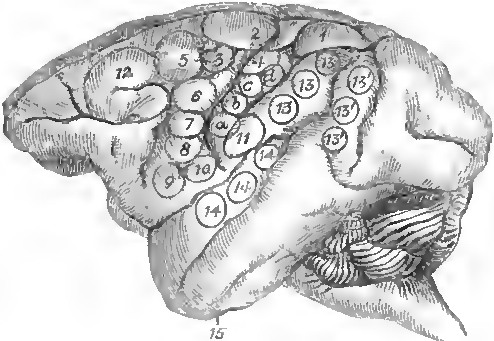


Fig. 3.