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EXPERIMENTS ON THE ELECTRICAL EXCITATION OF THE VISUAL AREA OF THE CEREBRAL CORTEX IN THE MONKEY.

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THE visual area of the cerebral cortex in the monkey, so far as it is determinable from the results of extirpation and of electrical excitation, comprises the whole of the occipital lobe. It perhaps includes a part or the whole of the angular gyrus, although the results of extirpation would appear to show, that the part played by the latter convolution is comparatively small. Removal of both occipital lobes produces total and permanent blindness, whereas destruction of the cortex of both angular gyri is not followed by any appreciable permanent defect of vision.¹ But, as will presently appear, electrical excitation of the posterior limb of the angular gyrus produces movements of the eyes similar to those which are produced by

¹ H. Munk, 'Verhandlungen der Berliner physiol. Gesellschaft,' 1878; and Schäfer, 'BRAIN,' January 1888. Of two monkeys in which, in conjunction with Dr. Sanger Brown, I completely removed both occipital lobes, leaving the angular gyri intact, one was totally blind and the other nearly so, having possession, however, of a small part of the visual field, so as to be able to see objects held well above the horizontal visual plane. On post-mortem examination it proved that the lesion did not in this case involve quite as much of the under-surface of the hemispheres as in the other. This agrees with the results of the excitation-experiments herein to be described, from which it will appear that stimulation of the under-surface of the posterior part of the hemispheres produces an upward inclination of the visual axes.

excitation of the adjoining portion of the occipital lobe; it is probably correct, therefore, to include at least this portion of the angular gyrus in the visual area.¹

The results which previous observers have obtained from excitation of the visual area as thus defined are contradictory. Ferrier obtained movements of the eyes to the opposite side with closure of the lid-openings, and contraction of the pupils, from excitation of the whole of the angular gyrus, the eyes being usually directed upwards when the electrodes were applied to the anterior limb, downwards when applied to the posterior limb. He "never obtained any reactions on stimulation of the occipital lobes."² Luciani and Tamburini got only the conjugate deviation to the opposite side without any constant upward or downward inclination, and they also obtained similar movements, but of a less marked character, on excitation of the convexity of the occipital lobe.³

I have carefully explored these parts of the hemisphere with the induced interrupted current in a number of monkeys, and have obtained the following results:⁴

¹ A similar result is obtained on stimulation of the upper end of the superior temporal gyrus, and of the adjacent portion of the middle temporal. This may be due, as is usually supposed, to the calling up of subjective auditory sensations; but the possibility of this part also belonging to the visual area, with which it is anatomically continuous, must not be overlooked.

Whilst engaged in enumerating the parts, excitation of which produces movements of the eyeballs, it is right that the frontal area for movements of the head and eyes should be included in the list. But this is evidently different (more direct) in its mode of action, for its removal causes paralysis of those movements (Ferrier), and moreover, as I have elsewhere shown ('Proc. Roy. Soc.,' 1888, and 'International Journal of Anatomy and Physiology,' 1888), its period of latency is much shorter than that of the posterior (visual and auditory?) areas.

² Ferrier, 'Functions of the Brain,' second edition, p. 244.

³ Luciani and Tamburini, 'Sulle funzioni del cervello. Centri psico-sensori corticali.' Reggio-Emilia, 1879. (Abstract in 'BRAIN,' Vol. II.)

⁴ For investigating the external surface, platinum-pointed electrodes of the ordinary pattern used in physiological experiments were employed; but for the exploration of the mesial and under surface, electrodes of a special pattern were constructed. These had their wires guarded, except on one side near the extremity, by paraffined paper, and were of such a form that they could be easily slipped between the brain and dura mater, and the excitation conducted through the unguarded parts of the wire directly to that part of the concealed surface which it was desired to stimulate.

A Du Bois-Reymond coil, with vibrating hammer, worked by a Daniell cell and with Helmholtz's side-wire inserted in the primary circuit, was used throughout. Ether was employed as an anæsthetic.

Excitation of the posterior limb of the angular gyrus, the upper end of the middle temporal gyrus (into which it is continued), and of the whole of the cortex of the occipital lobe, including its mesial and under-surfaces, produces conjugate deviation of the eyes to the opposite side. The excitable area also includes the part of the mesial surface immediately in front of the internal parieto-occipital fissure (quadrangle lobule). The movement produced is either a purely lateral one, or a lateral movement combined with either a downward or an upward deviation, according to the part to which the electrodes are applied.

1. When they are placed upon an area which includes the posterior limb of the angular gyrus, the part of the second temporal gyrus with which it is immediately continuous, the portion of the external surface of the occipital lobe immediately behind the external parieto-occipital fissure, and the anterior and upper part of the mesial surface immediately in front of (quadrangle lobule) and immediately behind the internal parieto-occipital fissure, the deviation is accompanied by a downward inclination, which is relatively most marked when the electrodes are applied on or near the mesial surface.

2. When they are placed upon an area which includes the posterior extremity of the lobe, its tentorial surface, and the posterior and lowermost part of its mesial surface, the deviation is accompanied by an upward inclination, which is also relatively most marked on applying the stimulation on or near the mesial surface.

3. When the electrodes are applied to an intermediate area, which is chiefly formed by the remainder of the convex external surface of the lobe, but also extends over the inner border to the mesial surface, where it becomes greatly narrowed, the deviation is simply lateral.

The results, therefore, of electrical excitation of this posterior (or visual) region of the hemisphere indicate a division into three zones; not sharply marked off from, but merging into one another. The first, or uppermost zone, is connected with downward inclination of the eyes; the second, or lowermost, with upward inclination; and the third, or intermediate zone, which is wide externally and narrow mesially, with a simple

lateral movement. But a lateral movement is also produced along with the downward or upward inclination by excitation of the upper and lower zones, although the vertical movement of the globes may be so powerful as almost to obscure the lateral inclination. This most frequently happens when the excitation is applied to the mesial parts of the upper and lower zones. Usually the upward direction of the visual axes, consequent upon stimulation of the lower zone, is accompanied by elevation of the upper eyelid, and the downward direction of the visual axes, consequent upon stimulation of the upper zone, by depression of the upper eyelid; but these effects have not been constant in my experiments, nor have the changes in the pupils which are sometimes observed accompanying the movements of the eyes.

I have not obtained any effect from stimulating, *with weak faradization*, the posterior limb of the angular gyrus, even when well-marked results have been obtained, with a strength of current barely perceptible to the tongue, from the parts which have just been considered.

I am unable to say exactly how far forward on the under-surface of the hemisphere these effects of excitation of the cortex may extend. The conjugate deviation to the opposite side, combined with upward inclination, is produced certainly as far as what is anatomically described as the limit of the occipital lobe on the under surface, and indeed the excitable region appeared to extend in advance of this limit; but it was not easy to say in experimenting upon this (concealed) part, to what spot precisely the electrodes had been applied.

I have occasionally obtained from stimulation on or near the quadrate lobule marked contraction of the pupils, such as is produced when a strong light is thrown directly into the eye. More usually, however, the movements, whatever the part stimulated, are accompanied by dilatation of the pupil.

So far as I have been able to observe, the visual axes always maintain parallelism when one side only of the hemisphere is stimulated. On one occasion I stimulated various corresponding points of the two hemispheres simultaneously. The result was usually a struggle between the muscles producing lateral movement, and the eyes either quivered without

moving to one side or the other, or the one set of muscles preponderated over the other, so that a lateral movement to one side resulted. In one case, when the electrodes were placed on corresponding points of the mesial surfaces, there was slight convergence of the visual axes; but this result was not sufficiently marked or constant to permit much stress to be laid upon it.

If we assume that these various movements of the eyeballs are the result or concomitants of subjective visual sensations set up by the excitation, and the movements take the directions towards which those sensations are projected, then the above experiments indicate a certain connection between the parts of the cerebral visual area and of the retinae. This connection may be stated as follows:—

1. The whole of the visual area of one hemisphere is connected with the corresponding lateral half of both retinae.

2. The upper zone of the visual area of one hemisphere is connected with the upper part of the corresponding lateral half of both retinae.

The lower zone of the visual area is connected with the lower part of the corresponding lateral half of both retinae.

4. The intermediate zone of the visual area is connected with the middle part of the corresponding lateral half of both retinae.

We may represent these relations diagrammatically, by supposing the visual areas of both hemispheres to be united at the great longitudinal fissure, and imagining each retina to be expanded and projected in its natural position upon the united area. If this is done, it is at once seen that the identical points of the two retinae correspond with one and the same spot of the cerebral cortex; that the upper half of each retina falls on the upper part of the united area, and the lower half of each retina on the lower part of that area; that the inner half of the one retina and the outer half of the other each fall upon the same hemisphere, and that a vertical zone, including the centres of both retinae, corresponds with the mesial part of the united area. This would connect the parts of the retinae which are concerned in direct or central vision with a part of the mesial surface of the occipital lobes, probably

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including a portion of the quadrate lobules. This scheme of connection between the retinæ and occipital lobes differs in several points from the well-known scheme formulated by H. Munk,¹ as the result of extirpation experiments, chiefly upon dogs, but partly upon monkeys. The most important differences relate to the extent of the visual area, and to the part of the occipital cortex which is connected with the central parts of the retina (macula lutea). The visual area (*Sehsphäre*) of Munk is *confined to the occipital lobes*, and the maculæ luteæ are *connected with the middle of the convexity of those lobes*.² Consequently, if the middle of the convexity of both occipital lobes is removed, central vision should be abolished. But, contrary to Munk, I have not found this to be the case in monkeys. Indeed, it was the smallness of the effect produced by this bilateral lesion which first led me to doubt the correctness of Munk's scheme. On the other hand, in one experiment which I have performed since obtaining the above results from stimulation of the cortex, there was a marked defect of central vision produced by a bilateral injury of both mesial surfaces. Complete and permanent abolition of central vision did not result, but it was found, post-mortem, that the lesion did not involve as much of the mesial surface of the visual area, especially upon one side, as was intended at the operation. It will be necessary to follow out the question more closely by the extirpation method, and this I intend in the near future to attempt; but the difficulty of arriving at reliable conclusions from localised extirpations of the visual area is enormous. For the animals soon acquire the habit of compensating for local defects in the visual field, by rapid movements of the eyes, so as to baffle all attempts to determine the existence of such defects. I believe, indeed, that to arrive at detailed conclusions we must await the results of perimetric observations in cases of cerebral lesion in the human subject, and that these experiments upon the visual area of the monkey are chiefly of value as affording indications of the kind of result which is to be looked for in man.

¹ H. Munk, 'Ueber die Functionen des Grosshirns,' *Gesammelte Mittheilungen*, Berlin. 1881, 5te Mittheilung.

² Op. cit. p. 127