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by Wesley Mills.**

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20

Cortical Cerebral Localization

WITH SPECIAL REFERENCE TO

RODENTS AND BIRDS

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III.—*Cortical Cerebral Localization, with Special Reference to Rodents and Birds.*

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Professor of Physiology in McGill University, Montreal.

(Read May 20, 1896.)

During the course of an investigation¹ on the "Functional Development of the Cerebral Cortex" in the Cat, the Dog, the Rabbit, the Cavy (Guinea-pig), etc., the question of the completeness and accuracy of the published researches on localization was often forced upon my notice, and never having found a cortical cerebral centre for the hind-limb in young rabbits, I was led to investigate this subject in the mature animal, and being unable to discover such a centre, it occurred to me that the whole subject of cerebral cortical localization in animals below the carnivora, at all events, was worthy of further study. Accordingly I have subjected the rabbit, the cavy, the rat, the mouse and the bird to experiments in order to determine the correctness and adequacy of existing views on localization.

I turned naturally to the classical work of Ferrier,² which gives this writer's views in a clear and concise form. This investigator defines a centre for movements of the hind-limb in the rabbit near the middle line and immediately behind that for the fore-limb. While my own work was in progress, Gustav Mann published a research on cortical localization,³ in which he attempted to deal with the subject in a manner more exact and complete than had hitherto been done. He also gives an account of the work previously accomplished by Ferrier and others. Apart from Ferrier's distinct statement, there does not seem to be very clear evidence in the literature of the location of a well-defined centre for the hind-limb.

Mann himself locates a centre for the hind-limb posterior to that for the neck and arm and near the middle line.

Speaking of his methods, Dr. Mann says: "As regards the *experimental part* of my research, the hedgehogs and cats were kept anæsthetized during the whole period of the experiment, while the rabbits were anæsthetized to render the preliminary operation painless, and then allowed to regain consciousness."⁴

¹ Published in these Transactions for the current year.

² "The Functions of the Brain," 2nd ed., London, 1886.

³ "On the Homoplasty of the Brain of Rodents, Insectivores and Carnivores," Journ. of Anat. and Phys., October, 1895.

⁴ *Loc. cit.*, p. 225.

He kept the experimental room at 75° F., and exposed both hemispheres fully, keeping the brain covered with absorbent cotton-wool when not being stimulated.

The only clue I can find to the reason for this difference in the method of treating the cat and the rabbit occurs in a sentence in which the work of another is referred to (p. 24): "I failed to produce accelerated breathing in non-anæsthetized animals."

Ferrier, speaking of stimulation, says: "Though it is obviously advisable to use no stronger current than is sufficient to produce a definite result, the measure of the intensity of the stimulus to be employed in each case is the degree of definite and decided localization of effects uniformly attainable."

He also says: "That (current) which will cause intense and indefinite action in an animal non-narcotized, will excite only moderate and definite action in an animal sufficiently narcotized to abolish all sense of pain, and no effect at all on an animal deeply anæsthetized."

I do not find that Ferrier anywhere recommends experimenting on non-narcotized animals, and from the last quotation I should suppose that he would be sceptical, to say the least, of results obtained in non-anæsthetized animals.

From a large experience in experimenting on the brains of animals, I can fully endorse all that is expressed in the quotations from Ferrier. Only experience can determine what degree of anæsthesia and what strength of current suit best.

My own methods in the determination of cerebral localization have been described in my paper on "The Functional Development of the Cerebral Cortex,"¹ so that only a brief reference need be made to them here.

The animals used, of whatever kind, were given ether. When fully under its influence the brain was exposed as rapidly and with regard to as little loss of blood, exposure to the air and other unfavourable conditions as possible.

It is true, as has been pointed out by Fürstner,² and quoted by Mann, that some movements may be induced by weaker currents than others, but following Ferrier's dictum, already quoted in regard to current, one centre may be compared with another under the same or very similar conditions without any danger of fallacy.

Mann states that he left his rabbits thirty to sixty minutes for the ether narcosis to pass off. Ether narcosis, as everyone knows, is comparatively transient, and it is because of this that I have used it invariably when conducting localization researches on the brain. Very frequently

¹ These Transactions for the current year.

² "Exper. Beitrag, z. Electrisch. Reiz. d. Hirnrinde" Arch f. Psych. vi. pp 719-732.

the animal is sufficiently from under its influence soon after the main operative procedure is over to allow of results being obtained at once, and unless the loss of blood be excessive I have always found it wise to proceed at once before the brain suffers by exposure.

However, after Dr. Mann's paper met my eye I determined to test his results by his own methods as regards the centre for the hind-limb in the rabbit, which I had never been able to find. The result agreed precisely with all my previous experience, to the effect that movements in an animal anaesthetized inadequately or not at all anaesthetized following on stimulation are hap-hazard. They may be in accord with those obtained under the use of an anaesthetic or they may be utterly delusive. It counts nothing with me that the same movement may be called forth over and over again on stimulating the same spot, for I have produced repeated movements of the hind-limb by stimulating the neck, area, etc.

Mann mentions that in one of his experiments on rabbits "both hind-legs kick out as in ordinary locomotion." (p. 26). Such a result in a mature rabbit should surely be viewed with grave suspicion, especially by one who claims such exact localization as Dr. Mann.

My own results on the rabbit may be thus briefly stated :

I have without any difficulty been able to localize cortical centres for a variety of movements for the fore-limb, the neck, head and face; with more difficulty, movements for the eyes and the ears; but in no single case when the animal has been properly under the influence of ether have I been able to get movements of the hind-limb by stimulation with any reasonable strength of current. A large number of animals of different breeding, some being cross-bred, some pure-bred, and some ordinary mongrels, and of varying age, have been employed.

I can only explain the positive result that some other investigators report by the assumption that their animals were not at the moment properly under the influence of an anaesthetic, and that a hap-hazard movement was mistaken for a genuine one. Certainly it would be strange, after so much experience in this kind of work and after subjecting this question of a centre for a hind-limb to special investigation with the use of so many animals of different breeding and age, that my results should be uniformly negative for this centre, but positive for all, or nearly all others found by experienced investigators, if I am in error. I can endorse what Fürstner¹ has said with regard to the ease with which chewing movements may be obtained in rabbits, and I have pointed out in my paper² on the functional development of the cortex that these and such like movements appear far earlier in the rabbit than in

¹ "Exper. Beitrag, z. Electrisch. Reiz. d. Hirnrinde." *Archf. Psych.* vi. pp. 719-732.

² These Transactions for the current year.

the dog and the cat; in fact, that they may be induced about as soon as those for the fore-limb.

To my mind it is perfectly clear that it cannot be maintained that the movements for the hind-limb are in the same relation to the cortex in the rabbit as are those for the fore-limb and the face. Whether the centre exists, but is too ill-organized to be susceptible to stimulation by our rough experimental methods, whether it is too readily disordered by operative procedure to allow of experimental determination I do not know, but I am satisfied that to represent such a centre as of the same kind and demonstrable in the same way as others in the rabbit is a mistake. In some respects it would remove difficulties if such a centre could be demonstrated to exist, but on the other hand it must be borne in mind that the method of locomotion in the rabbit is peculiar and is not comparable to that of the rat, cavy (guinea-pig), etc.

As regards the cavy and the white rat I can confirm in general Ferrier's localization. I have also examined the brown rat and the mouse and find that their cortical centres correspond in the main with those of the white rat and the cavy.

I have made a sufficient number of experiments on mature cats and dogs to enable me to confirm in a general way the usually accepted localization. I wish, however, to point out that there is a certain degree of individuality as regards the exact position of the centres in the dog and the cat, and perhaps still more in the readiness with which they may be excited by electrical stimulation. The same may be said as to the effects of ablation.

In regard to the latter, I do not find any functional defect of a kind that prevents the animal walking within a very short time after operation. There is, however, a change in the animal's movements—sometimes at first a tendency in dogs and cats in the fore-limb to bend under and for both the fore and the hind limbs to slip and to scrape on the surface over which the creature walks. The latter was especially noticeable in cats from which the motor areas around the crucial sulcus on both sides were completely removed by one operation. Nevertheless, even in such cases, the animals rapidly improved. Soltmann's¹ explanation—loss of muscular sense—in my opinion, goes a long way to explain this, though I would not deny that there is also *some* loss of muscular power.

In rabbits and other rodents the localization is less definite than in the dog and the cat, and it seems to me a mistake to omit to state this in any work on cortical localization. In my experience the centres are not nearly so definitely marked off and are more variable in exact position. Certain movements, however, just as constantly and readily follow on

¹ *Jahr. f. Kinderheilkunde u. Phys. Erziehung*, 1876.

weak stimulation in the rabbit at all events as the corresponding ones in the dog and cat, if not more so. These are the very movements that are most frequently called into exercise by the life habits of the animals, and it seems to me important to recognize that all cortical centres are not equally well organized, as might be inferred from reading the accounts of some authors on this subject. This applies to the whole question of cortical localization and not to that of the rabbit alone, though, as I have shown, it is specially well illustrated in this animal.

In my attempts to carry the investigation of cortical cerebral localization downwards in the animal scale I naturally reached the bird. Upon turning to Ferrier's account¹ I found that he claimed that stimulation of an area in the upper parietal region caused "intense contraction of the opposite pupil, occasionally associated with turning of the head to the opposite side." He further says: "In a few cases I have also observed, from stimulation of the region below this, turning of the head to the opposite side without contraction of the pupil. Beyond these effects the results of stimulation were entirely negative."

I have made a thorough examination of this subject in the pigeon, and have investigated the case of the fowl sufficiently to convince me that there is no difference, at all events so far as the main results are concerned.

The methods employed were the same as for other animals, and the results may be stated briefly as follows:

Every part of the cortex is refractory to stimulation, so far as movements of the neck, head parts and limbs are concerned. This also applies to the white matter lying beneath the cortex.

Stimulation of the cortex may give rise to contraction or to dilatation of the pupil, or produce little or no change in it in either eye. When a change occurs, it is usually greatest on the opposite side, and may be practically confined to that side.

The result may be momentary or last for an appreciable time—may be a steady effect or oscillatory. Very rarely, if ever, can it be maintained for any considerable period.

As to whether contraction results or not seems to depend, to some extent, on the condition of the pupil at the time; for the result has been more frequent when the pupil has been already moderately dilated. Contraction has been more frequent than any other effect. I have not been able to demonstrate the conditions under which dilatation takes place, nor the one effect now, and the other again, as sometimes occurs. Both dilatation and contraction may occur during experiments made on the same bird. Apparently the conditions are complex and variable.

¹ "The Functions of the Brain," 2nd Ed. London, 1886.

The most constant effect of stimulating the cerebral cortex in the pigeon I have found to be movements of the nictitating membrane. In all cases this structure has been drawn down over the eyeball to a greater or less extent, and if the current used be sufficiently strong, the membrane may be held over the eyeball for a brief period.

The effect is greatest on the opposite side, but is not usually confined to that side.

The eyelids are usually drawn more or less together at the same time, though this effect is much less constant and pronounced than that just noticed.

The area of stimulation which produces these effects and those on the pupil is not a very well defined one, but corresponds fairly well with that indicated by Ferrier. I have frequently got more marked movements of the nictitating membrane on excitation of a point a little more forward and outward. The same results follow on stimulating the underlying white matter of the cerebrum.

I may say, finally, in regard to the pigeon, that it is very important that the bird be properly under the influence of an anæsthetic, as even in birds not wholly under the influence of ether there may be movements of the head on applying an electrical current or a stream of water to the brain.

The variability in the result as regards the pupil may be dependent in part on the degree of anæsthesia and the varying manner in which the nervous mechanism of the eye is affected, and this is, I am inclined to think, a partial explanation of the unsteadiness of the results, though individual differences must also be recognized. For myself I have not been greatly surprised at this variability, considering the nature of the nervous mechanism of the eye, composed as it is of antagonistic elements, which probably vary a good deal functionally in individuals and during anæsthesia.

GENERAL CONCLUSIONS.

In the dog, cat, rabbit, cavy, rat and mouse, electrical stimulation of the cerebral cortex over definite regions produces regularly certain movements.

These animals are, however, not on the same physiological plane with regard to this subject.

The dog and the cat are more closely related, and fall into a physiological group by themselves; the rabbit, the cavy, the rat and the mouse constitute another group.

There are well defined differences for the cat and the dog. The same applies to the members of the other group.

In the cat and the dog the motor areas are better defined than in the members of the other group.

In the case of all these animals it has been clearly demonstrated that all motor centres are not functional equivalents—some respond more readily and produce better defined movements than others. They seem to be better organized.

There appears to be all degrees of this functional variation down to zero. The rabbit is an especially good illustration of some phases of this principle.

The cortical localization mapped out by Ferrier for the dog, cat, rabbit, cavy and rat is in the main confirmed by the present investigator, but considerable allowance must be made for individual differences, and it is important, as has been just pointed out, to recognize that all motor centres in the same animal are not functionally equivalent in the sense explained above.

The removal of motor centres in the animals made the subject of this investigation does not lead to complete loss of the corresponding movements, and in some cases the difference between the intact animal and that operated on is, after a few days, relatively slight; so that it is plain that motor centres in such animals are not strictly comparable with motor centres in the *Primates*. In other words, here again the question of degree of localization and functional organization (among others) must be considered.

The bird is on a wholly different plane. None of the ordinarily recognized movements on stimulation of the cerebral cortex can be excited in the bird. On the other hand, certain eye movements, both intrinsic and extrinsic, follow as a result of stimulation of the cortex.

