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Phenomena Resulting from Interruption of Afferent and Efferent Tracts of the Cerebellum

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II. *Phenomena resulting from Interruption of Afferent and Efferent Tracts of the Cerebellum.*

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(*From the Pathological Laboratory of University College, London.*)

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1. Introduction.

I am greatly indebted to Professor Victor Horsley for allowing me to carry out the investigations, the results of which are embodied in this paper, in the Pathological Laboratory of University College, London.

My object in undertaking this research, was twofold, as I wished in the first place

to obtain evidence in support of or against the view that the cerebellum exercises a direct influence on the spinal centres, as opposed to any indirect influence exerted through the agency of the cerebral cortex, and in the second place to ascertain whether any descending tract could be traced from the cerebellum, by way of which any such direct influence could be brought to bear on the spinal centres. It is, however, impossible for me to do more than deal with the first of these problems in the present paper.

In a former paper, dealing with ablation experiments on the cerebellum, I showed that while some of the effects obtained might result from the altered excitability of the cerebral cortex, which was demonstrated to exist, it was impossible to avoid the conclusion that others were the result of the removal of a direct influence which the cerebellar centres normally exerted over those of the spinal cord. The best way to obtain positive evidence on this point appeared to be to divide the inferior cerebellar peduncle on one side, leaving the organ itself and its other peduncles otherwise intact; this has accordingly been done; and the results obtained form part of the present communication. It however quickly became apparent that to perform this operation without injury to the auditory nuclei, and without including some fibres of the superior peduncle in the lesion, was no easy task.

It seemed desirable, as a control, to ascertain whether the effects obtained on section of the inferior cerebellar peduncle were also to be obtained when a section of the lateral region of the medulla was made between the posterior column nuclei and olive, so as to interrupt the direct cerebellar and lateral medullary tracts, without implicating the posterior columns or their nuclei; and these results have been in their turn controlled by experiments in which a transverse section was made, including the posterior columns and their nuclei on one side a few millimetres above the level of the calamus scriptorius.

Further control experiments consisted in performing almost complete hemisection of the medulla about 3 or 4 millims. above the calamus scriptorius, the pyramid being alone excluded from the section. The knife entering the medulla from the middle line posteriorly was made to pass through the organ in such a way as to divide all structures on one side with the exception of the pyramid. In other instances, the olive was excluded from the section also, the knife entering in the middle line from behind, as in the last case, but being brought out at the lateral region by the medulla just dorsal to the region of the olive.

2. Historical Review.

Numerous as have been the experimental investigations into the functions of the cerebellum, the middle are the only peduncles of the organ to which attention has specially been directed by any number of experimental physiologists. Very few observers have made the inferior peduncle the subject of separate investigation.

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Laborde* found that injuries of the restiform tracts caused disorders of equilibration similar to those caused by lesions of the semicircular canals.

Ferrier and Turner† destroyed the left inferior peduncle in one monkey by the galvano-cautery, and divided it in four others, after which there was incurvation of the vertebral axis to the left. The left limbs were adducted and flexed, and the right extended and abducted. Attempts at movement occasioned rolling from right to left. Knee-jerks were equal and normal. There was no loss of sensibility. No ocular deviation was present, except in one case, but in two of the animals there were nystagmoid movements of the globes.

Biedl‡ divided the restiform body and ascending root of the fifth nerve on the left side in cats, and found that no paralysis resulted, but that there were marked disturbances of co-ordination in the extremities on the side of the lesion and in the head and neck muscles.

3. Plan of Experimentation.

I. Division of the Inferior Cerebellar Peduncle on one side.
II. Partial Section of the Lateral Region of the Medulla on one side (control).
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    (B.) Partial Hemisection of the Medulla.
V. General convulsions induced by Intravenous Injection of Absinthe—
    (A.) One Inferior Cerebellar Peduncle divided;
    (B.) Partial Hemisection of the Medulla;
    (C.) Transverse Section of the Posterior Columns and their Nuclei on one side.

4. Operative Procedure.

In all the experiments, the animals were first placed under the anæsthetic influence of ether, which was administered by inhalation, and the narcosis was continued until the end of the experiment, when the animal was killed under its influence. In those cases in which it was necessary to allow the animal to live after the operation, and where there was any likelihood of any pain resulting, morphia was administered, by subcutaneous injection, before the anæsthetic influence of the ether had passed off. Such animals were killed under the influence of ether at the end of the time that it

* Laborde, 'Compt. Rend. de la Soc. de Biol.,' 1882, p. 427.
† Ferrier and Turner, 'Phil. Trans., Roy. Soc.,' 1894, p. 749.
‡ Biedl, 'Wiener Klin. Woch.,' 1894, Nr. 46.

was necessary to observe the symptoms resulting from the lesion. Tracheotomy was performed in all cases where it was not intended to allow the animal to live after the subsequent operative and other procedures. The external jugular vein was exposed on one side of the neck in those instances where absinthe was to be administered.

A single longitudinal incision was made in the middle line at the back of the head and neck, and the muscles cut and scraped away from their attachments to the occipital bone and upper cervical spines. The muscles were divided and scraped away as equally as possible on the two sides, so as to exclude the possibility of any rotation or twisting of the head in some direction being due to the action of muscles having their attachments intact on one side, while the corresponding muscles of the opposite side had been separated from their attachments. Bone forceps were alone used to effect an opening into the cranial cavity and neural canal, and after opening the theca the posterior part of the cerebellum was carefully separated from the medulla oblongata and raised to the extent necessary for the performance of the section of the inferior peduncle of the cerebellum as it enters the organ, or for the division of the posterior columns and their nuclei, and the tracts which occupy the lateral region of the medulla, or to perform partial hemisection of the medulla. In those instances in which a section of the lateral region of the medulla was made it was further necessary to make gentle traction on the medulla so as to displace it slightly to the opposite side in order to allow of the possibility of accurately delimiting the extent of the lesion. The actual section of any part was made by means of a narrow-bladed delicate knife.

When it was necessary to expose the cerebral cortex an opening was effected into the cranial cavity, at some point away from the motor areas for the limbs, by means of a small trephine, and the opening was subsequently enlarged by means of bone forceps. Every possible precaution was taken to avoid injury to the cortex, and the two hemispheres were treated exactly alike, so as to place them in precisely the same condition; they were kept warm and irrigated with warm normal salt solution throughout the excitation experiments.

In every instance in which it was intended that the animal should be allowed to survive the operation, this was done under the strictest possible antiseptic precautions. The skin was first shaved, thoroughly cleansed by soap and water, and afterwards well scrubbed with perchloride of mercury lotion (1–1000). The same strength of lotion was used for sponging out the wound during the operation until the stage at which the dura mater was about to be opened was reached, from which point boiled normal salt solution was alone used, so as to exclude the possibility of any myelitic complication arising from the action of the antiseptic lotion on the nerve structures. At the termination of the operation the external wound was once more sponged out with perchloride of mercury lotion, and then the whole washed carefully with normal salt solution. The edges of the skin wound were brought together by aseptic horse-hair sutures, a small opening being left at the most dependent part for drainage, the

surface of the skin again washed with perchloride of mercury lotion, and an antiseptic dressing applied.

When absinthe was used with a view to evoke convulsions in the animal, three to six minim doses of the essential oil were injected into the blood stream by way of the external jugular vein.

Electrical excitation of the cerebrum was effected by means of fine closely approximated platinum-pointed electrodes attached to the secondary coil of a Du Bois-Reymond's inductorium supplied by a single bichromate cell.

The records of muscular contractions were taken, in the case of the anterior extremities, from the extensor muscles of the wrist and digits, while in the case of the posterior extremities they were taken from the sural muscles. In either case the muscles and tendons were freely separated from the bones and other underlying structures to a considerable longitudinal extent, and the tendons of the two limbs attached to two Fick's spring myographs whose springs were as nearly as possible of equal strength. The writing points of these were of the same length, and were made to record on the blackened surface of paper stretched between two revolving cylinders kept in motion by means of a clock.

5. The Effect of Division of One Inferior Cerebellar Peduncle.*

In these experiments the peduncle was always divided as high up as possible, as it enters the cerebellum, in the hope that the fibres contained in the peduncle might alone be severed without any injury being done to the auditory nuclei in the medulla. The task of dividing the peduncle in this way was by no means as simple as might be expected, for it was found exceedingly difficult to divide the peduncle high enough to avoid injury to the auditory nuclei, and yet not so high as to include in the lesion parts of the cerebellum other than the fibres entering and leaving it by its inferior peduncle. Often when the appearances as seen with the naked eye seemed to indicate that this object had been attained subsequent microscopic examination showed that one or other of the auditory nuclei had been more or less injured. Then, again, the knife readily passed too far forward so as to sever fibres leaving the cerebellum by the superior peduncle; the higher the inferior peduncle was divided the more tendency was there for this complication to occur.

Attitude.—This was exceedingly characteristic, consisting in arching of the neck and trunk with the concavity to the side of the lesion so that the head and tail were approximated. There was little or no rotation of the head about the longitudinal horizontal axis of the body. The curving of the trunk becomes most obvious when the animal is disturbed, as when attempts are being made to induce it to stand. Under such circumstances, if the trunk be forcibly straightened it quickly

* The term "inferior cerebellar peduncle" is intended to include the restiform body and Edinger's direct sensory cerebellar tract.

returns to its former curved condition directly the force exerted to straighten it is taken off. Further, if for instance the left peduncle be divided the animal lies on its left side when at rest, and resists all attempts which may be made to place it to lie on its right side. If this resistance is forcibly overcome and the animal is placed to lie on its right side, it quickly rolls on to its left side directly the restraining force which is exerted to keep it on its right side is taken off. Sometimes so suddenly and vigorously does it roll over to the left side that it may, as it were, overstep the mark and roll over once or twice before coming to rest on its left side. The position of the limbs also calls for some comment. As the animal lies on its left side the usual condition in which they are found is one of flexion of the left extremities and extension of the right; but when it is disturbed all the extremities are usually extended. This last statement requires qualification however, for although true of what usually happens when the animal is first disturbed, it does not hold good throughout the examination, for it was found that the left hind limb, at any rate, was then held in a flexed condition when the animal was placed on its right side, or on its back.

All these conditions which have been described were most marked directly after the operation, and were characteristically present twenty-four hours later, when they can be most conveniently and satisfactorily examined, as presumably the animal may then be regarded as having recovered from the effects of the anæsthetic, and most of the shock consequent on the operation has passed off.

With regard to the spasm present in the limbs it is always exceedingly difficult, if not impossible in some cases, to distinguish between involuntary spasm of the muscles and voluntary spasm induced by the animal, owing no doubt to a sense of insecurity consequent on the lesion, and the uncertainty as to what is likely to take place during the examination.

When there was rotation it took place about the animal's longitudinal axis towards the side of the lesion, that is to say, in a left-sided lesion, the animal rotated like a right-handed screw entering an object; while in a right-sided lesion it rotated like a similar screw coming out of an object.

Disorders of Motility.—There is at first a complete inability to assume the standing position, and when attempts are made to place the animal to stand on its limbs, it fails entirely to support itself by them, and invariably falls over on to the side of the lesion. There appears to be an entire loss of all knowledge of how to use the limbs to support the body. When the left peduncle is divided the right limbs are at first usually kept extended, and the left more or less flexed; and even later when there is less of the spasmodic flexion of the left extremities, if an attempt is made to place the animal on all fours the left limbs appear to double up under it and it falls to the left side. The major part of these defects are unquestionably due to two factors, loss of muscular sense or the sense of position, and rigidity; but it is impossible to do otherwise than believe that another factor responsible for the inability on

the part of the animal to stand is what is commonly known as motor paresis. The way in which the limbs on the side of the lesion appear to give way and double up under the animal when it is placed on all fours makes it difficult to avoid this conclusion. Further, as the animal recovers and first begins to stand it can only do so by supporting the side of the lesion against some steady object, such as on the walls of the room in which it is being examined. Then again, when it is possible for it to stand without such support it does so on a wide base, the limbs, both anterior and posterior, but more especially the latter, being widely separated from each other. If it attempts to shake itself, the limbs, more particularly the left, *i.e.*, on the side of the lesion, slide away from under the trunk, and the animal falls on to its left side. When it attempts to walk it does so in a sprawling manner, and as it further improves it becomes more and more possible, up to a certain point, to detect the uncertainty which exists with regard to the use of the limbs on the side of the lesion, and it is further possible to detect that when the animal falls, the posterior extremity on the side of the lesion is that which gives way first. Later, the animal becomes quite active, and walks and even runs about in an uncertain and ataxic manner, repeatedly falling on to its left side owing to the limbs on that side not being properly under the animal's control. The motor paresis does not affect all the limbs equally, but is most marked in the posterior extremity on the side of the lesion, less marked in the anterior extremity of the same side, and still less marked in the opposite posterior extremity, while the opposite anterior extremity appears to escape entirely. And, as has already been said, when power is being regained in the extremities the posterior extremity on the side of the lesion is that in which it is last restored.

Ocular Displacements.—Few facts in connection with the results of division of one inferior peduncle of the cerebellum are more definite than is the displacement of the globes which is to be seen after such a lesion. After the animal has recovered from the effects of the anæsthetic, both eyes are seen to be displaced downwards and to the opposite side from that on which the peduncle has been divided. If the left peduncle is divided, the displacement of the right eye is unquestionably greater than that of the left, especially as regards the degree of its displacement to the right; but in this connection, it has to be remembered that in the dog more sclerotic is visible on the inner than on the outer side of the cornea, and that, therefore, any displacement of the eye outward obtrudes itself on the observer more than does any displacement of the eye inward. Allowing for this source of fallacy, however, I still feel justified in stating that after division of one inferior peduncle the outward displacement of the opposite eye is greater than the inward displacement of the eye on the side of the lesion. Further, like all the other effects resulting from such a lesion, recovery takes place within a variable time, and in process of recovery it is invariably the eye on the side of the lesion which first returns to its normal position, the outward displacement of the opposite eye being obvious for a considerable time

after the inward displacement of the eye on the side of the lesion has ceased to be detected.

The degree of displacement of the globes varies considerably in different animals; in some it is well marked, while in others it is slight; but in all it is present. So, too, the rate of improvement varies to a similar degree in different dogs, in some it passes off in a few days, while in others there is still some evidence of its existence, at any rate in the eye on the side opposite to that of the side of the lesion, two weeks after the operation. The time that the displacement persists largely depends on its degree in the first instance, those cases in which it is slight recovering more rapidly than those in which it is pronounced soon after the operation.

Apart from the actual displacement of the globes, and, indeed when this no longer exists, or is trivial, the animal appears to be unable to direct its eyes to the side of the lesion; at any rate, all attempts to induce it to do so, as a rule, fail, while it can be readily induced to direct its eyes to the opposite side when they are not very obviously displaced in this direction, or to turn them still further to this side, when the displacement, the result of the lesion, is considerable.

Further, even in those cases when there is only slight displacement of the globes after the operation, or where displacement has existed, but has recently been recovered from, the displacement can be brought about by placing the animal in some position in which, from its general behaviour, it is obvious that it is suffering from a sense of insecurity from loss of balance. When speaking of the attitude common to dogs in whom the inferior peduncle of the cerebellum has been divided on one side, for instance the left, I stated that such animals prefer to lie on the left side, and that they resist all attempts which may be made to place them on their right side; now when such attempts are made to place the animal to lie on its right side, this is one of the occasions when the abnormal displacement of the globes is intensified.

I have purposely avoided any mention of the position of the eyes in such animals after division of the inferior peduncle while they are still under the influence of the anæsthetic, because mention of this in my former paper on the cerebellum led to some misunderstanding, in that I was taken to mean that the displacement then observed was characteristic of the lesion, which was far from my intention. The only displacement of the eyes that can be regarded as truly characteristic of the lesion is that which exists after all influence of the anæsthetic has passed off. But there is another effect of the anæsthetic to which I wish to allude, and that is its influence with regard to the position assumed by the eyes after all displacement, the result of the operation, has passed off, and the animal is again placed under the anæsthetic influence of ether. In the stage which precedes that in which the eyes diverge—the stage, in fact, in which the eyes of normal dogs are displaced to one side or the other—the eyes of such dogs are displaced to the opposite side from that of the lesion, and this irrespective of the side to which they turned in the same stage of narcosis before the peduncle was divided. The effect of the anæsthetic in

such animals, then, is to reproduce, at a certain stage of anæsthesia, the ocular displacement which at one time existed as a result of section of one inferior peduncle of the cerebellum.

Nystagmus.—Spontaneous nystagmus is rarely observed when the animal is at rest, but when disturbed and placed in some position in which it does not feel secure—as, for instance, when placed to lie on its right side when the left inferior peduncle has been divided—nystagmus is rarely absent during the first few days after the operation. As has been already said, any disturbing element responsible for increasing the animal's sense of insecurity increases the ocular displacement, and with this nystagmus usually results. The jerks are in the direction opposite to that of the ocular displacement; thus, if the eyes are displaced downwards and to the right, the nystagmoid jerks are upward and to the left. Of these two elements in the direction of the jerks, the upward usually is the more marked, but the combined effect adds a certain degree of rotation to the movements of the globes.

Sometimes the nystagmus occurs alone, but at other times it is accompanied by blepharospasm, constant blinking movements of the eyelids occurring simultaneously with the ocular jerks.

Reflexes.—Of all the phenomena which result from division of one inferior peduncle of the cerebellum, none are so difficult to be certain about as is the alteration in the state of the tendon reflexes. This difficulty is largely due to the amount of spasm of the muscles of the limbs, voluntary or otherwise. It is rarely possible to get the limbs sufficiently relaxed to be certain that the full effect of the response, as a result of the blow to the patella tendon, is being obtained. However, there seems little doubt that both knee-jerks are increased in activity as a result of the lesion; but the question does not end here, for it next becomes necessary to ascertain whether one knee-jerk is more increased than the other, and here comes the chief difficulty. Difficult as it is to get the animal to relax the muscles of one limb satisfactorily, it is still more difficult to obtain an equal degree of relaxation on the two sides at the same time, so that the most varying results are obtained; at one moment the one jerk appears to be the greater, at another moment the other. So that it is only by long, careful, and repeated observations that it becomes possible to venture on an opinion as to which knee-jerk is really the more active. Making all allowances for the difficulties which have to be overcome and fallacies to be guarded against, I am left with the impression that the knee-jerk on the side of the divided peduncle is greater than that on the opposite side; but I make the statement with great reserve, as, in the face of such difficulties, it is impossible to make a positive statement in this connection.

Disorders of Sensibility.—The extreme difficulty of testing sensation in animals, or rather of coming to definite conclusions with regard to the presence or absence of cutaneous sensibility, makes it important that we should only record those facts with regard to which there appears to be no question. In dogs I find it most difficult to

be certain with regard to sensibility to tactile and thermal impressions, while there is very little difficulty in ascertaining accurately the condition as regards painful impressions. I therefore prefer to limit my observations at present to the state of sensibility to painful impressions. In testing this a metallic clip was used, of such strength as to be objected to by normal animals in a manner which left no room for doubt as to whether the animal, which was of course, blindfolded, was or was not aware of its presence on some portion of its cutaneous surface. Normal dogs tested in this way invariably objected when the clip was placed on any of the four extremities, and as far as could be ascertained the skin of the four extremities was sensitive to an equal degree to the stimulus.

Dogs in whom the inferior cerebellar peduncle was divided on one side gave evidence of most marked departure from this normal standard. For a variable time after the operation, usually about a week, the animal takes no notice of the clip when it is placed on any of the extremities, and that not only when the skin alone is pinched up, but when the clip is firmly pressed against the periosteum of some bone. The limb in which sensibility to painful impressions usually returns first is the anterior extremity of the side opposite to that of the lesion. There appear to be few exceptions to this rule in uncomplicated cases. The posterior extremity on the side of the lesion, on the other hand, is, as a rule, the last to recover; but it is less easy to speak definitely with regard to the order of restoration of sensibility to painful impressions in the other extremities; sometimes the posterior extremity of the opposite side, at other times the anterior extremity on the side of the lesion, is the second to recover. But in spite of this fact of the posterior extremity on the side of the lesion being last to recover when sensibility to painful impressions returns in all the extremities, the animal may appear to be more sensitive to painful impressions on the posterior extremity of the side of the lesion than on the opposite side.

When sensibility to painful impressions is first returning the animal only takes notice of the clip when it is pressed firmly against the periosteum of some bone; but, as further improvement occurs, the pinching up of the skin alone is objected to, and in the end they respond to the stimulus in the same way that normal dogs do. There is always return of sensibility to painful impressions before the improvement in motility is sufficient to allow the animal to stand or walk.

6. The Effects of Partial Section of the Lateral Region of the Medulla on one side interrupting the Lateral Medullary and Direct Cerebellar Tracts (Control).

The section of the medulla was made transversely and in such a way as to avoid injury to the posterior columns and their nuclei on the one hand, and the pyramid on the other. In order to accomplish this successfully a narrow-bladed delicate knife

was inserted just external to the posterior columns, its point was brought out just externally or dorsally to the inferior olive, and the knife was then made to cut its way out of the portion of the medulla thus transfixed.

Attitude.—The attitude assumed by such an animal, after it had recovered from the effects of the anæsthetic, resembled closely that of a dog whose inferior cerebellar peduncle had been divided close to the point where it enters the organ. The neck and trunk were curved with the concavity of the curve to the side of the lesion, but the curving of the neck was much more pronounced than was that of the trunk. There was, however, no twisting of the head by rotation of the neck on its longitudinal axis so as to turn either side of the animal's face upward. If the neck and trunk were forcibly straightened they quickly returned to their abnormal position when the restraining force was taken off, and it was easy to satisfy one's self that the curving of the neck and trunk with the concavity of the curve to the side of the lesion was due to an actual spasm of the muscles on that side of the body.

There was inability to stand or walk, and the animal evidently felt more secure when placed to lie on the side of its body corresponding to the lesion than when placed to lie on the side opposite to the lesion. The latter procedure resulted in only a limited portion of the animal's body remaining in actual contact with the ground, for the curving of the neck and trunk was exaggerated under these circumstances, and thus the head and posterior quarters of the animal became approximated to each other and both were raised off the ground. When there was rotation of the animal, which did not always occur, it did so round its longitudinal axis like a right-handed screw entering an object when the lesion was on the left side, a direction which, according to my previous descriptions I have regarded as rotation to the side of the lesion.

Disorders of Motility.—These closely resembled those which resulted on section of the inferior peduncle of one side at its point of entrance into the cerebellum.

The animal was at first unable to stand, and in all attempts to do so the posterior extremities remained flexed under it, but it raised the fore part of its body by means of its anterior extremities. This position was, however, only momentarily maintained, as the anterior extremity on the side of the lesion quickly doubled up under the animal and as a result it invariably fell over on to that side. As the animals recovered the posterior extremity on the side of the lesion was the last in which power was restored, and there were many ways in which this was shown. Such an animal after apparent recovery will sometimes stand on three legs and scratch its head with the posterior extremity on the side of the lesion, while it will make no such attempt to stand on three legs while using the opposite posterior extremity to scratch its head with. Indeed, I have seen such animals, after scratching with the posterior extremity on the side of the lesion while standing on the other three extremities, deliberately lie down and then scratch the other side of their heads with the opposite posterior extremity.

Then again, if the animal happens to be a male, long after it appears to have regained motor power completely, it makes no attempt to pass urine in the way common to most male dogs, that is by raising one posterior extremity; on the contrary such dogs invariably urinate like puppies, simply lowering the posterior part of the trunk by flexing the posterior extremities.

These supplementary remarks with regard to evidences of defective power more especially in the posterior extremity on the side of the lesion, though made here, apply equally to those animals in which the inferior cerebellar peduncle has been divided on one side close to the cerebellum.

Ocular Displacements.—The positions of the globes depended largely on the exact extent of the lesion. If the lesion was extended far enough forward so as to include the whole of the direct cerebellar tract, then the position of the globes was similar to that which resulted when the inferior peduncle was divided close to the cerebellum, that is, both eyes are turned downwards and away from the side of the lesion, this being well marked in the opposite eye and only slightly evident in the eye on the side of the lesion. In those cases on the other hand in which the lesion was limited, involving only the lateral region of the medulla in close proximity to the posterior columns without dividing the direct cerebellar tract, the eyes were displaced to the side of the lesion instead of to the opposite side, and this displacement was more pronounced in the globe on the side of the lesion than in the opposite one. There was, however, the same element of downward rotation of the globes in both instances.

The ocular displacements could be intensified by putting the animal in some position in which it evidently felt insecure, as for instance by placing it to lie on the side of the body opposite to that of the lesion.

As in the displacements of the globes which result from lesions of the cerebellum or its inferior peduncle, so in the case of section of the lateral region of the medulla the ocular displacement was only temporary and was gradually recovered from, so that, as a rule, within a week of the time of the operation the eyes recovered their normal positions.

Nystagmus.—No nystagmus was detected when the animal was at rest, and even when the animal was placed in some position which appeared to increase its feeling of insecurity, and which resulted in an intensification of the ocular displacement, no nystagmus was observed.

Reflexes.—The same difficulty which was met with in testing the knee-jerks after division of the inferior cerebellar peduncle was encountered in the case of these experiments also. The posterior extremities were so constantly held in a state of flexor spasm when an attempt was being made to elicit the knee-jerks, that it was really quite impossible to arrive at any positive opinion as to the full degree of their increased activity, and as to which of the jerks was the more increased; but as far as could be judged, the left jerk appeared to be slightly the more active of the two. In some

animals there could be little question as to the left being the greater, but in others it was exceedingly difficult to be certain.

Disorders of Sensibility.—The day after the operation such an animal took no notice of the painful clip when this instrument was placed on any of the extremities, and this condition of analgesia persisted for some time after the operation, finally clearing up in the same order, as regards the four extremities, as has been detailed in connection with section of the inferior cerebellar peduncle. The opposite anterior extremity is that on which the animal first begins to take notice of the clip, and the posterior extremity on the side of the lesion is the last in which there is evidence of return of sensibility to painful impressions. As in the case of the inferior peduncle, so here there was a good deal of variability as regards which of the other two extremities first recovered sensibility.

7. The Effects of Transverse Section of the Posterior Columns on One Side a Few Millimetres Above the Calamus Scriptorius (Control)

Dogs on whom this operation was performed presented a very different picture to those in whom the inferior peduncle was divided close to the cerebellum, or in whom the lateral tracts of the medulla were severed. The lesion was effected by means of a delicate narrow-bladed knife, which was made to enter the middle line of the medulla posteriorly, about two or three millimetres above the calamus scriptorius, and to pass transversely outwards, so as to divide both the funiculus gracilis and funiculus cuneatus with their respective nuclei.

Attitude.—The animals were, as a rule, able to stand and walk a few hours after they had recovered from the effects of the anæsthetic. The trunk was curved, with the concavity to the side of the lesion, as in the case of division of the inferior cerebellar peduncle. The neck was also curved, with its concavity in the same direction, and the head was twisted on the trunk, so that one or other side of the face was turned to a varying degree upward, while the other side of the face was, of course, turned downward; but the same side of the face was not always turned upward, for while in most cases that on the side of the lesion was so turned, in other cases it was the opposite side of the face which was turned upward. When the latter was the case, it was not so pronounced, however, as when the side of the face corresponding to the side of the lesion was that which was turned upward.

Disorders of Motility.—In standing and in walking the posterior part of the trunk was at a lower level than the anterior, owing to the posterior extremities being kept in a semiflexed condition. This gave the animal a curious appearance during progression, which was rendered still more striking by the fact that in moving forward the dog did so sideways, like a crab, so that the side of the lesion was constantly kept facing towards the direction in which the animal was walking.

These defects were gradually recovered from, the twisting of the head on the neck

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and the arching of the trunk being the first to pass off. The position of the posterior extremities and the inclination to keep the side of the lesion forward during progression were more lasting symptoms, and did not entirely pass off in some cases until a fortnight had elapsed after the operation.

Ocular Displacements.—The reverse of what obtains in the case of a lesion of the inferior cerebellar peduncle was met with in these cases where the posterior columns on one side were divided, for the eyes were displaced to the side of the lesion instead of to the opposite side. The two lesions have one thing in common in this connection however, in that in both cases the eyes were directed downwards. As in the case of the peduncle, so here, the displacement was not equally marked on the two sides, but, whereas in the former case it was the opposite eye that was most displaced, in the case of the posterior columns it was the eye on the side of the lesion which was most obviously displaced.

When such animals were induced to look to the side opposite to that of the lesion, the opposite eye moved better and farther in that direction than did the eye on the side of the lesion.

The ocular displacement was recovered from in the course of a week, the opposite eye recovering before that on the side of the lesion.

Even after they had recovered, however, and could be moved well to either side, traces of the former defect could be detected when the animal was lifted, placed on its back or side, or otherwise suddenly disturbed or agitated.

So too, if placed under the anæsthetic influence of ether after the eyes had returned to their normal positions, the displacement downwards and to the side of the lesion was reproduced during the stage of narcosis which immediately preceded that in which the eyes diverged.

Nystagmus.—The occurrence of nystagmus was certainly not the rule; there was, however, one case in which it was present, but here the lesion was not limited to the posterior columns, but extended more deeply so as to injure the lateral region of the medulla. In the case in question there was well-marked lateral nystagmus, and the eyes were displaced to the side of the lesion as in other cases of transverse section of the posterior columns on one side, and not to the opposite side as in the cases in which all the lateral tracts of the medulla were divided and the posterior columns and their nuclei were left intact.

Reflexes.—There appeared to be some increased activity of the knee-jerks, though not to the same extent as after division by the inferior peduncle of the cerebellum high up or section of the lateral tracts of the medulla. It was exceedingly difficult to be certain of any real inequality of the knee-jerks owing to the fact that there always appeared to be a certain amount of flexor spasm of the posterior extremity on the side of the lesion, while the muscles of the opposite posterior extremity were much more relaxed during the examination. How much of the flexor spasm in the posterior extremity on the side of the lesion was voluntary and how much involuntary

it was difficult to estimate. When the muscles of the limb on the side of the lesion were relaxed, the knee-jerk on that side appeared to be more active than that on the opposite side; but the difficulties which attended the examination made it impossible to speak with any degree of certainty on a point where comparatively slight differences were being dealt with.

Disorders of Sensibility.—As in the case of the experiments on the inferior cerebellar peduncle so in these experiments, I confined my attention entirely to the presence or absence of the power of conduction of painful impressions. A few hours after the operation, when the animals had so far recovered from the immediate effects of the operation as to be able to walk a little, though imperfectly, they took no notice of the clip when this was placed on any of the extremities. This defective conduction of painful impressions was still evident on the following day, but afterwards began to show signs of improvement. The order in which the limbs recovered in this respect was quite constant, but the tendency appeared to be for the anterior extremities to recover before the posterior, and for the limbs of the opposite side to recover before those on the side of the lesion.

8. Comparison of the Electrical Excitability of the Two Cerebral Hemispheres.

(A.) *One Inferior Cerebellar Peduncle divided.*

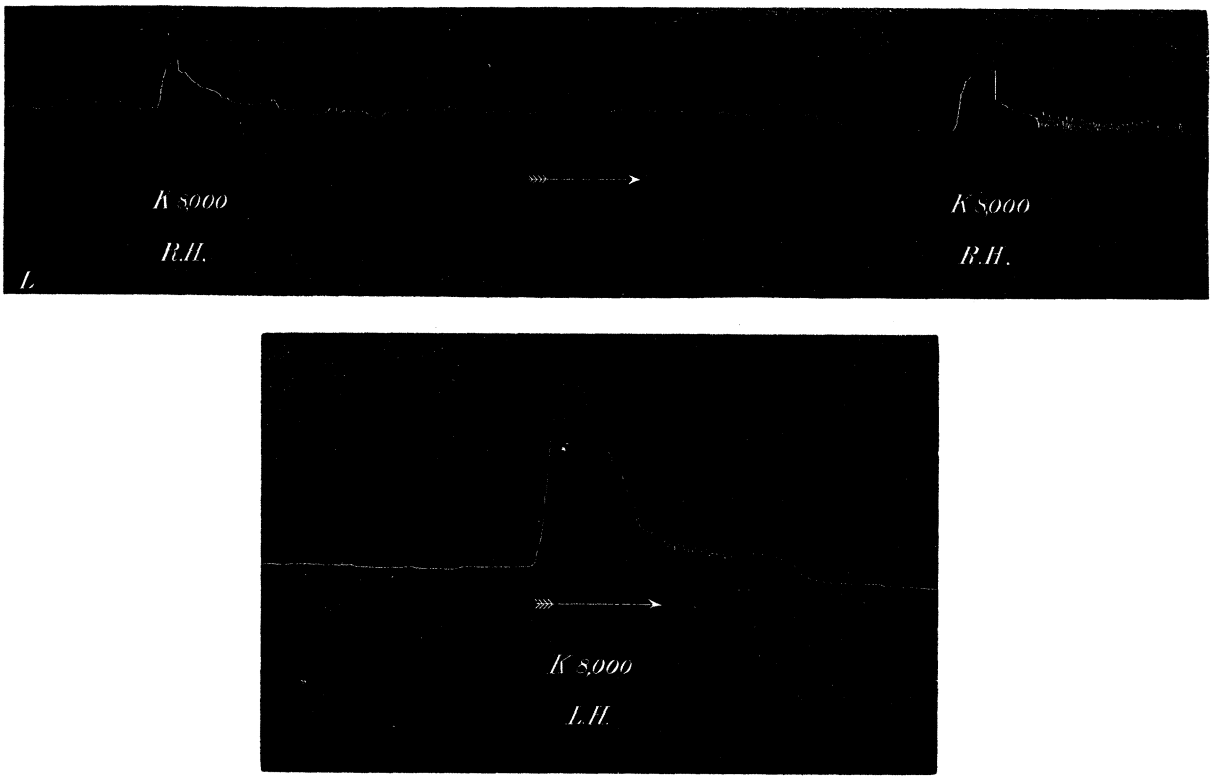
The greatest possible care was taken not to injure the cortex on either side when the cerebral hemispheres were being exposed, and to avoid any pressure on the cortex. The two hemispheres were placed as far as possible in exactly the same conditions, and the cortex of each was kept warm and irrigated from time to time with warm normal salt solution.

The extensor muscles of the anterior extremities were exposed, separated from their attachments to the lower two-thirds of the bones of the forearms, and while their proximal attachments were left intact the distal ends of their tendons were divided and connected with spring myographs, whose springs were as nearly as possible equal, and records of the muscular contractions were taken in the way that has been described earlier in this paper.

The time at which the inferior cerebellar peduncle on one side was divided varied; sometimes this was the first part of the operation, at other times it followed the exposure of the extensor muscles of the forearm, and at other times it followed the exposure of the cortex of the cerebral hemispheres, which part of the operation was always preceded by exposure of the extensor muscles. At whatever period in the course of the operation the peduncle was actually divided, the exposure of the cerebellum and preparation for subsequent division of the peduncle was always the first step undertaken.

Testing of the electrical excitability of the cortex always followed immediately on the completion of the various preliminaries that have just been detailed. The fore-limb area of each hemisphere was carefully explored in order to find, if possible, a focus in each excitation of which most readily resulted in a response from the extensor muscles of the fore limbs. At other times, a point as nearly as possible in the same position on the two sides was chosen, and the excitability of the cortex at this point on each side carefully tested. The results obtained by the one method of procedure were thus checked by those obtained by the other method.

Fig. 1.



Records of response obtained when the cortex of the cerebral hemispheres was excited with a current of 8000 on KRONECKER'S scale, soon after section of the left inferior peduncle of the cerebellum.

R = right anterior extremity. L = left anterior extremity.
R.H. = right cerebral hemisphere. L.H. = left cerebral hemisphere.

The results varied according to the extent of the lesion of the inferior peduncle, that is to say the more completely was the peduncle divided, the greater was the difference of excitability of the cortex noted on the two sides. This only held good as long as the lesion was strictly limited to the inferior peduncle, however, for although this might be completely divided, the effect would be considerably modified if any considerable portion of the fibres of the superior cerebellar peduncle were also included in the lesion.

So long as the lesion was limited to the fibres of the inferior peduncle on one side, the greater the completeness of division of this structure the less excitable was the opposite cerebral hemisphere as compared with its fellow, and as tested by the response obtained from the extensor muscles of the fore-arm of the anterior extremity of the animal. So that if the left inferior peduncle was the one divided, the response from the extensor muscles of the left fore-limb on excitation of the right cerebral hemisphere, was less than the response obtained from the muscles of the right fore-limb on excitation of the left cerebral hemisphere. Thus in an experiment in which

Fig 2.

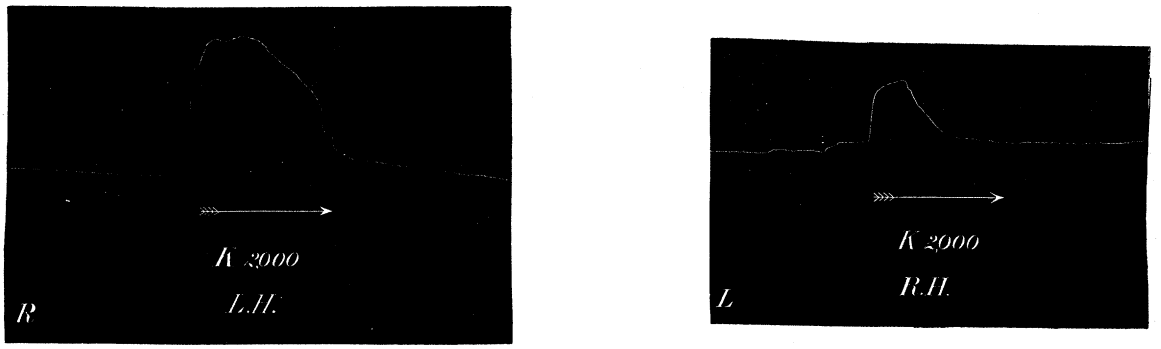
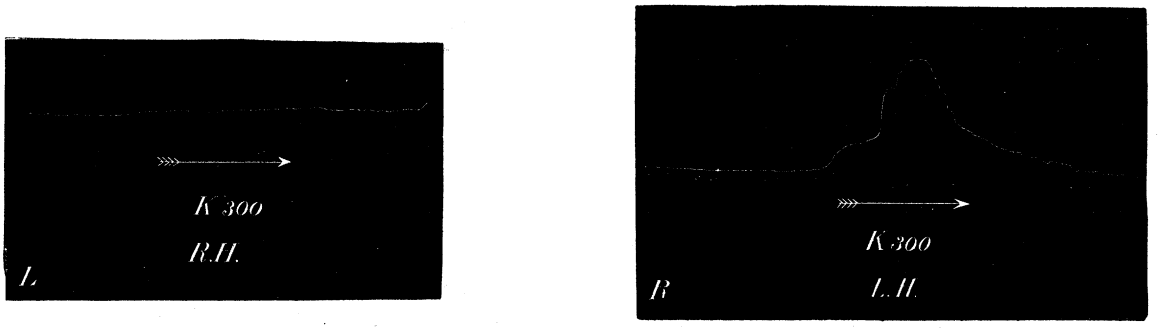


Fig. 3.



Records of response obtained from the extensor muscles of the fore-arms on stimulation of the cortex of the cerebral hemisphere with a current of 2000 and one of 300 on KRONECKER'S scale, in an animal soon after section of the left inferior cerebellar peduncle.

R. = right anterior extremity. L. = left anterior extremity.
R.H. = right cerebral hemisphere. L.H. = left cerebral hemisphere.

the left inferior peduncle was divided, an induced current with the secondary coil at 400 on KRONECKER'S scale, and with the inductorium supplied by a single bichromate cell, failed to elicit any response in the extensor muscles of the left fore-limb when the right cerebral hemisphere was excited, while the same current when applied to the left cerebral hemisphere evoked well-marked contraction in the extensor muscles of the right fore-limb. Then again in an animal in which the same lesion had been produced, an induced current with the secondary coil at 8000 on KRONECKER'S scale,

gave a greater response in the extensor muscles of the right anterior extremity on excitation of the left cerebral hemisphere than resulted in the muscles of the left anterior extremity when the right hemisphere was excited (see fig. 1). The same result was obtained with the secondary coil at 4000 and at 2000 (see fig. 2), while with the secondary coil at 300 on the same scale, there was no response from the extensor muscles of the left fore-limb when the right hemisphere was excited, while the muscles of the right anterior extremity responded distinctly when the left cerebral hemisphere was stimulated (see fig. 3).

(B.) *Partial Hemisection of the Medulla.*

In one series of experiments instead of dividing the inferior peduncle close to the cerebellum, partial hemisection of the medulla on one side about 3 or 4 millims. above the calamus scriptorius was performed. In this operation the knife was passed from the middle line posteriorly through the whole thickness of the medulla from behind forward, but slightly obliquely so as to just avoid injury to the pyramid, it was then made to cut its way out of the medulla transversely. In some cases the pyramid appeared to escape injury completely, while in others a variable number of the outer fibres of this structure were included in the lesion.

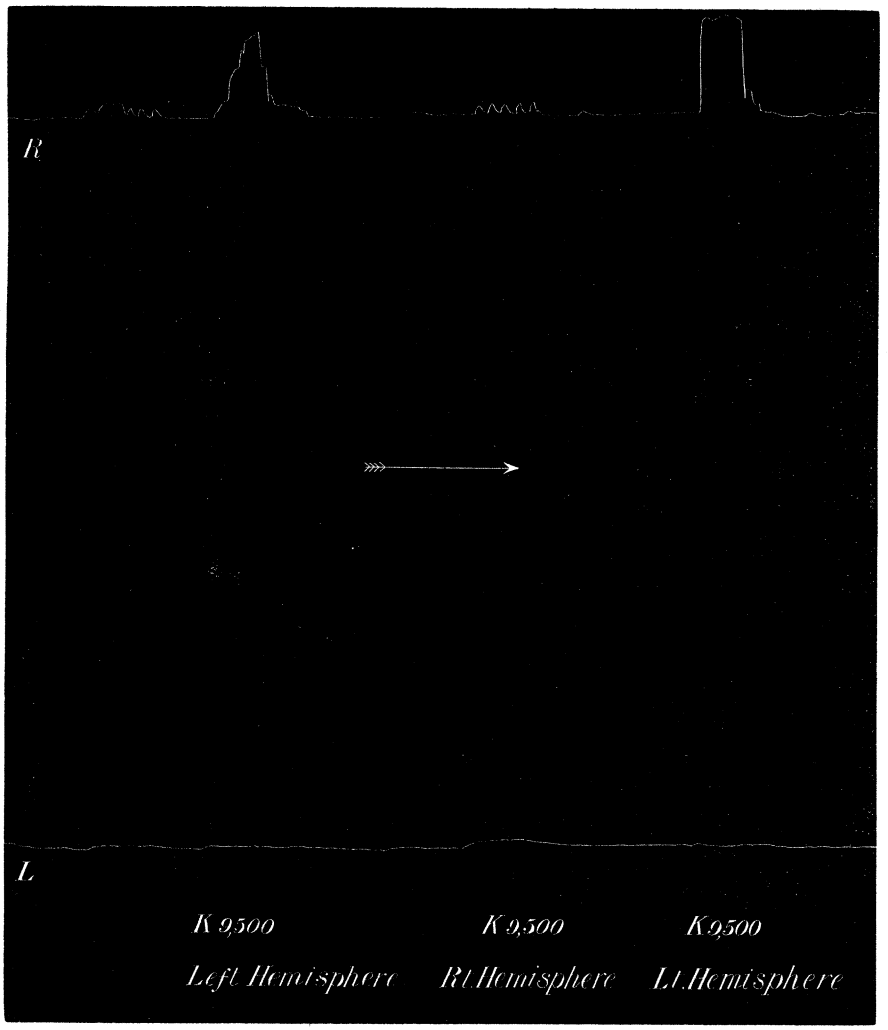
When the lesion was on the left side and the pyramid escaped, or the injury to it was only trivial, induced currents of sufficient intensity to evoke a response from the extensor muscles of the right fore-limb when the left cerebral hemisphere was excited, failed to elicit any response in the muscles of the left fore-limb when the right hemisphere was stimulated.

But not only was a difference in the excitability of the two hemispheres observed when stimuli of moderate intensity were employed, but also in some cases when stimuli of sufficient intensity to evoke general epilepsy were used. Under these circumstances a stimulus applied to the left cerebral hemisphere, when the left inferior peduncle was divided, evoked general epileptic spasms in which all the muscles of the body appeared to be involved except those of the left anterior extremity, the exposed extensor muscles of whose fore-arm remained quite passive throughout the otherwise general convulsions. Although the muscles of both posterior extremities were in spasm under these circumstances, it was easy to see that those of the left posterior extremity were contracting less vigorously than those of the right posterior extremity.

Striking as was this result, in which the muscles of the fore-limb on the side of the lesion remained passive during otherwise general epileptic convulsions induced by excitation of the cortex of the cerebral hemisphere concerned chiefly with the production of movement on the opposite side of the body, it was still more remarkable to find that even a current of sufficient intensity to evoke general epileptic convulsions when applied to the opposite cerebral hemisphere, that is, that concerned chiefly with

the movements on the side of the body on which the hemisection of the medullar has been performed, failed to elicit contraction in the extensor muscles of the anterior extremity on the side of the lesion.

Fig. 4.



Records of response obtained from the extensor muscles of the fore-limbs, on stimulation of the cortex of the cerebral hemispheres with a current of 9,500 on KRONECKER'S scale, in an animal soon after lateral section of the medulla on the left side.

R = right anterior extremity; L = left anterior extremity.

Fig. 4 is a record of the contractions of the extensor muscles of the right anterior extremity of an animal in whom partial hemisection of the medulla was performed on the left side, and shows that, with a current of 9,500 on KRONECKER'S scale, applied to the left hemisphere, well marked contractions resulted in the muscles of the right anterior extremity, while the muscles of the left anterior extremity recorded no such contractions when the same strength of current was applied to the right cerebral hemisphere.

9. Convulsions induced by Intravenous Injection of Absinthe.

(A.) *One Inferior Cerebellar Peduncle divided.*

(1.) Immediate Effect.
(2.) Remote Effect.

In my former paper it was shown that absinthe convulsions induced in normal animals resulted in muscular contractions which had the same characters on the two sides of the body, so that tracings taken from the extensor muscles of the fore-limb of the dog showed clonus, followed by tonus ending in clonus. In animals in whom the inferior peduncle of the cerebellum was divided on one side, a striking alteration was observed, the precise nature of which depended on whether the convulsions were induced immediately after section of the peduncle or at some remote period.

Immediate Effect.

(1.) The immediate effect was much the more striking of the two, and consisted in an entire absence of convulsions in the muscles of the anterior extremity on the side of the lesion. Not only did the writing-point of the spring myograph not record any contractions of the muscles, but by direct observation it was easy to satisfy myself that the muscles of this extremity remained inactive, while all the other muscles of the animal seemed to be actively contracting. When tracings were taken of the convulsions in the posterior extremities, they showed no such remarkable difference on the two sides; but the convulsions in the muscles of the limb on the side of the lesion were less powerful than were those in the opposite posterior extremity.

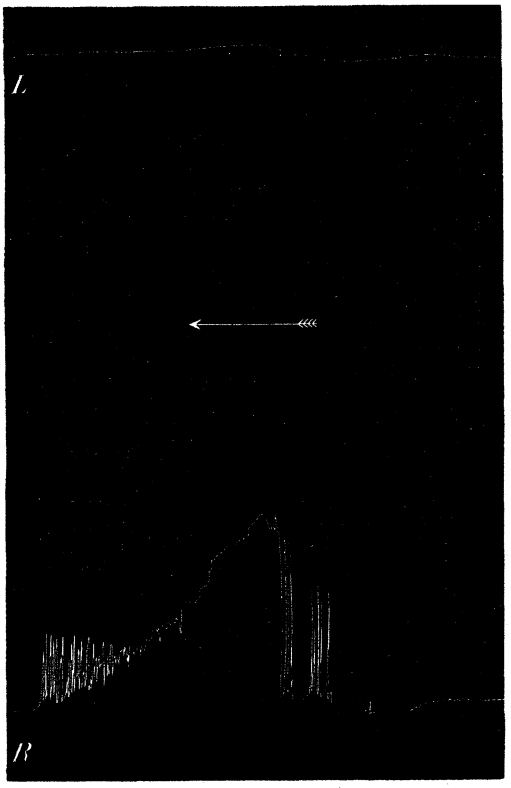
Fig. 5 shows this effect very clearly, the records being taken from an animal in whom the left inferior cerebellar peduncle was divided, and absinthe convulsions were induced at the time of the operation, that is soon after the section of the peduncle. Here it may be seen that while the extensor muscles of the right anterior extremity recorded well-marked convulsions, there is absolutely no sign of the record of a convulsion in the extensor muscles of the left anterior extremity, the writing-point of the spring myograph with which they were connected recording a more or less straight line throughout the period, during which the writing-point of the other myograph was recording the active muscular contractions of the extensor muscles of the right anterior extremity.

In all cases the muscles first connected with one myograph were afterwards connected with the other, and further epileptic convulsions induced in order to exclude the possibility of one myograph being more easily acted on than the other, and thus accounting for the remarkable difference observed in the records from the two fore-limbs. This precaution was superfluous, however, for as has already been

said, direct observation of the exposed extensor muscles, during the epileptic convulsions, alone served to place beyond doubt the fact that the muscles of the right extremity were in vigorous contraction, while those of the left extremity remained absolutely passive.

Not only was this effect observed in the first or first few convulsions evoked, but provided the division of the inferior peduncle had been fairly complete, and the lesion had not involved, to any extent, the fibres of the superior peduncle, it could be repeated time after time in a series of convulsions of considerable number.

Fig. 5.



Result of convulsions induced by absinthe in an animal soon after the left inferior peduncle of the cerebellum was divided. Tracing obtained from extensor muscles of fore-arm.
R = right. L = left.

(2.) *Remote Effect.*

If, instead of inducing convulsions in the animal a short time after the inferior peduncle on one side was divided, it was allowed to live for three weeks or so, and the convulsions evoked in it by intravenous injection of absinthe, the state of things which resulted differed very markedly from that met with when the convulsions were evoked immediately after the section of the peduncle. There was no longer an absence of convulsions in the extensor muscles of the anterior extremity of the side of the lesion, but, nevertheless, the character of the convulsions in the two anterior

extremities differed in important respects, as shown by tracings obtained by means of the spring myographs. Such tracings showed a much greater degree of tonic convulsion in the muscles on the side of the lesion as compared to those of the anterior extremity of the opposite side, where there was much less tonus, its place being taken by clonic contractions. Like the immediate effect, these differences could be made out without the aid of the tracings, by direct observation of the exposed extensor muscles of the fore-limbs on the two sides. In addition to this difference as regards tonus and clonus on the two sides, the contractions of the muscles of the left anterior extremity were less powerful than were those of the right anterior extremity. Indeed, in cases in which practically no other differences in the characters of the convulsions could be detected on the two sides, this difference in the amount or power of contraction could be well seen. Fig. 6 is the record of the contractions of the extensor muscles of the two anterior extremities of a dog whose inferior peduncle was divided on the left side about three weeks before the records were obtained. General epileptic convulsions were induced by absinthe, and, as may be seen from the figure, while there was very little difference as regards clonus and tonus on the two sides, the amount of power of contraction on the right side was much in excess of that on the left. In such experiments, as in the case of the former ones, the myographs were always subsequently reversed, the muscles first connected with one myograph being afterwards connected with the other, to exclude the possibility of the differences in the character of the recorded contractions being due to any differences in the springs of the myographs. In all cases the tension of the strings connecting the muscles with the myographs was kept as nearly as possible equal on the two sides.

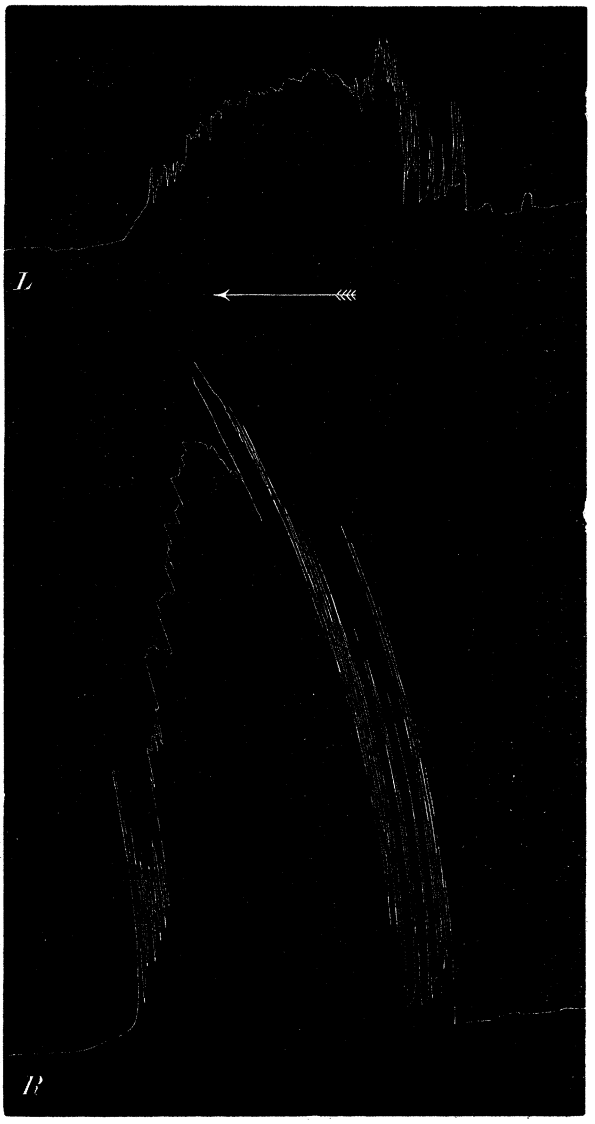
Such were what may, for convenience of description, be called the pure immediate and remote effects of section of one inferior peduncle of the cerebellum in modifying the convulsions induced by absinthe. These results were, however, only obtained when the lesion was fairly limited to the inferior peduncle and yet divided the greater portion of this structure. The fewer the fibres divided in the peduncle the less likely were these effects to be observed, and the more other parts of the cerebellum, especially the superior peduncle on the same side, were involved in the lesion, the more likelihood was there that these phenomena would not result. Indeed in those cases where the extension of the lesion to the superior peduncle was at all serious, both the immediate and remote effects observed during absinthe convulsions showed a greater degree of contraction in the extensor muscles in the fore-limb on the side of the lesion than in that of the opposite side, the reverse of what was obtained in lesions limited to the inferior peduncle on one side.

(B.) *Partial Hemisection of the Medulla.*

Hemisection of the medulla so performed as to divide all the structures on one side with the exception of the pyramid led to modifications in the results of the

absinthe convulsions as remarkable, and indeed identical with those observed after section of one inferior peduncle of the cerebellum. There was the same absence of contraction of the extensor muscles of the fore-limb on the side of the lesion during

Fig. 6.



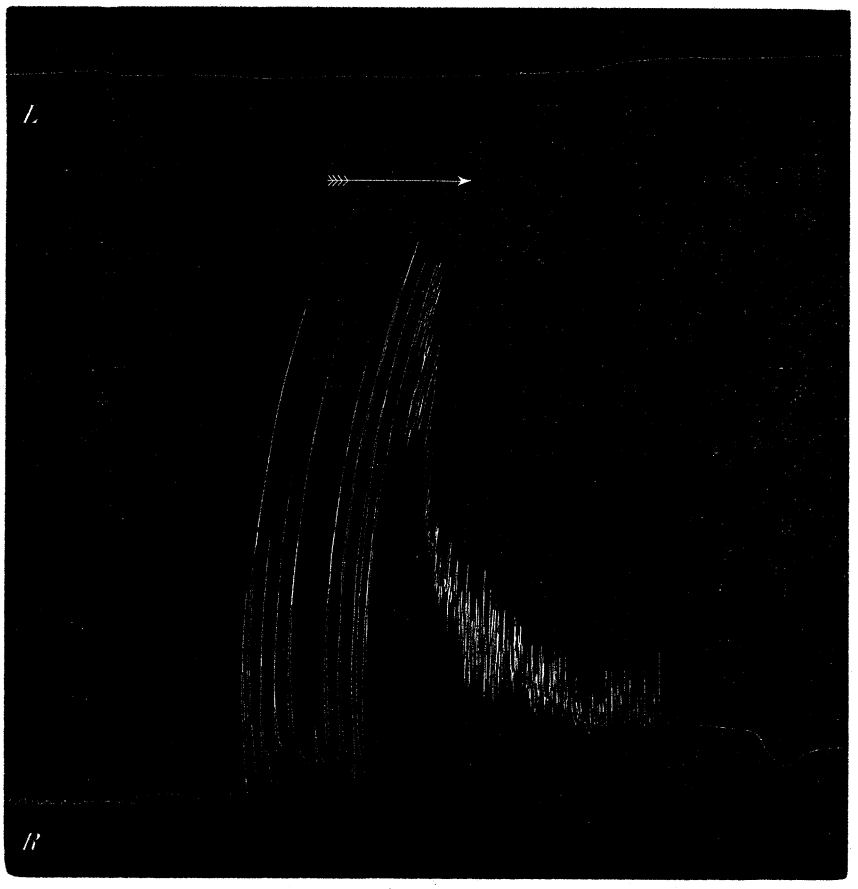
Result of Convulsions induced by absinthe in an animal three weeks after the left inferior peduncle of the Cerebellum was divided.

R—right anterior extremity. L—left anterior extremity.

otherwise general convulsions in which the extensor muscles of the opposite anterior extremity took an active part. As in the case of the inferior peduncle, so here, not only did the records obtained with the myograph indicate this difference, but actual observation of the exposed muscles left no room for doubt that the records gave a

true account of what was actually taking place in the muscles of the limbs, those of the anterior extremity on the side of the lesion being quite passive and free from spasm of any kind. The well-marked muscular contractions of the extensor muscles of the right anterior extremity are well shown in fig. 7, which is a tracing taken from an animal in whom partial hemisection had been performed on the left side of the

Fig. 7.



Result of convulsions induced by absinthe in an animal in whom partial hemisection of the medulla was performed a short time before the tracing was taken.
R = right anterior extremity. L = left anterior extremity.

medulla a short time before the convulsions were evoked by absinthe, and which shows equally clearly how the writing-point of the myograph connected with the extensor muscles of the left anterior extremity preserved a comparatively straight line during the time that these vigorous muscular contractions were going on in the opposite fore-limb.

The resemblance between the effects of partial hemisection of the medulla and division of one inferior peduncle of the cerebellum, were further borne out by the way in which the absinthe convulsions affected the muscles of the posterior extremities, for the muscles of both these limbs were in active contractions during the convulsions,

but the contractions of the muscles on the side of the lesion were less powerful than were those on the opposite side.

In some instances a considerable number of the fibres of the pyramid were accidentally divided with the other structures on one side of the medulla, in which case the extensor muscles of neither anterior extremity contracted in some instances, and while the muscles of both posterior extremities contracted, those of the opposite limb did so less powerfully than did those of the limb on the same side as the lesion.

(c.) *Transverse Section of the Posterior Columns and their Nuclei on one side.*

The lesion in these cases was made in such a way as to include the *funiculus gracilis* and *funiculus cuneatus* with their nuclei, without extending so far forward as to divide the lateral medullary and direct cerebellar tracts.

Absinthe convulsions induced in animals in whom this operation had been performed, showed a difference in the characters of the curves representing the contractions of the extensor muscles of the two anterior extremities, but both the immediate and remote effects resembled the remote effect produced by division of the inferior cerebellar peduncle on one side rather than the marked effect so characteristically seen when convulsions are evoked in an animal immediately after the inferior peduncle has been divided on one side. The extensor muscles of both forelimbs contracted during the absinthe convulsions, but the muscles of the limb on the side of the lesion contracted less powerfully than did those of the opposite side, and there was more tonus in the muscles on the side of the lesion, there being no clonic contractions in these muscles in some instances. Fig. 8 shows the early effect in an animal whose posterior columns and their nuclei were divided on the left side, and absinthe convulsions induced two weeks afterwards. The tracing shows clearly how the muscular contractions of the left anterior extremity were not only smaller in amount than those on the right side, but also largely tonic in character, as opposed to the large amount of clonus shown in the tracing of the muscles on the right side.

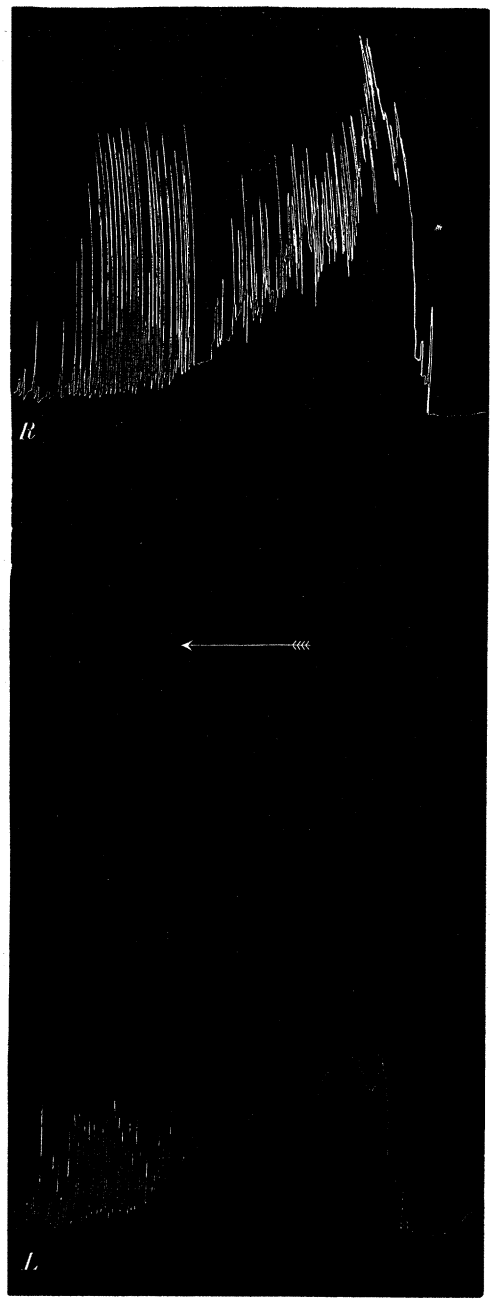
Fig. 9 represents the same condition of things in an animal in whom absinthe convulsions were induced about two weeks after the posterior columns and their nuclei were divided on the left side, the record being one taken towards the end of a long series of convulsions of which fig. 8 is a representation of one of the earlier ones. This figure shows how much the amount of contraction becomes diminished on the left side, and how all clonus is absent from the convulsions on that side.

10. Discussion of Results.—Conclusions.

The phenomena which result from section of one inferior peduncle of the cerebellum considered in conjunction with former results which I obtained from ablation of one lateral half of the cerebellum, and others from intracranial section of the auditory

nerve, appear to me to afford us valuable information with regard to many of the functions of the cerebellum; but they cannot be said to settle definitely the all-important question as to whether the cerebellum exercises a direct downward

Fig. 8.



Result of convulsions induced by absinthe in an animal two weeks after division of the left posterior columns and their nuclei in the medulla. The tracings represent one of the earliest of a series of convulsions.

R = right anterior extremity. L = left anterior extremity.

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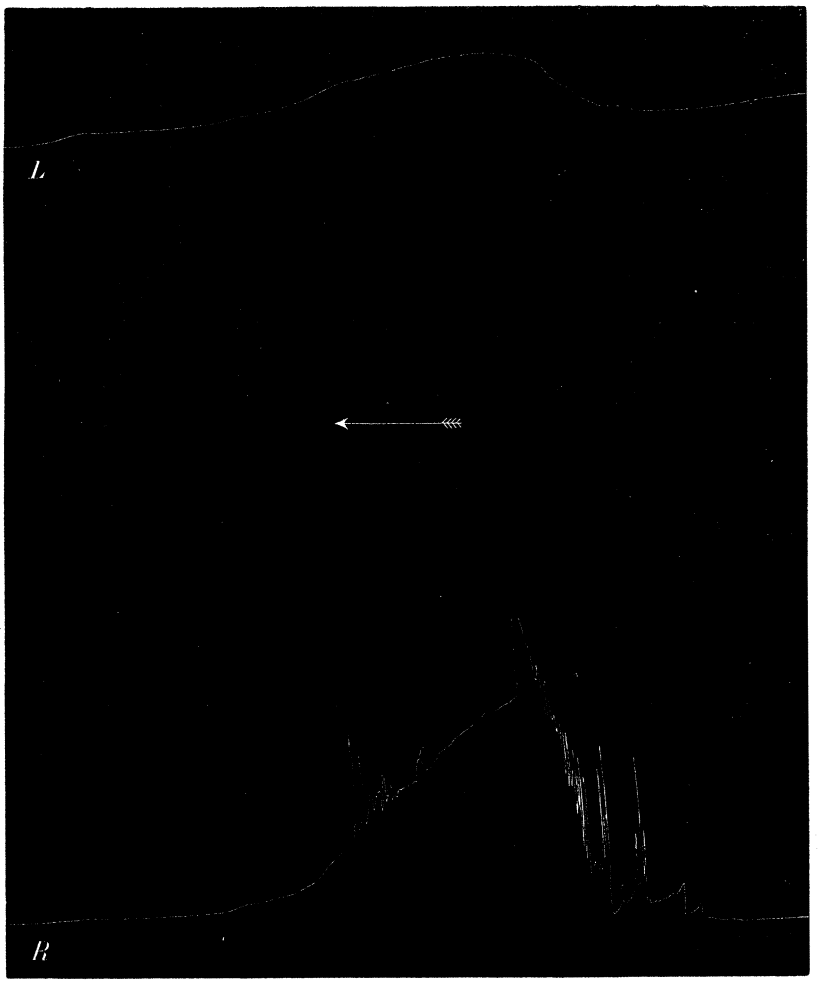
influence on the spinal centres or not. Many of the results obtained by division of one inferior peduncle of the cerebellum suggest the possibility of such a downward influence, as was also suggested by the results of ablation of one lateral half of the organ; but none of them can be claimed as absolute and incontrovertible evidence of the existence of such an influence exercised by the cerebellum on the spinal centres,

Fig. 9.



Result obtained towards the end of a long series of convulsions induced by absinthe in an animal two weeks after division of the left posterior columns and their nuclei in the medulla.
R = right anterior extremity. L = left anterior extremity.

and through them on the muscles. All the effects which point to this possibility can as readily be explained by supposing that they are the result of the cutting off of afferent impulses from the periphery towards the cerebellum as a centre, as will become evident if we briefly review the effects obtained.

That the disorders of co-ordination are the result of the interruption of afferent

impulses passing from the periphery to the cerebellum does not admit of much doubt. It is interesting to note that whereas an animal deprived of, for instance, the left half of its cerebellum rotates like a right-handed screw coming out of an object (what I have described as rotation away from the side of the lesion), one in which the left inferior peduncle of the cerebellum is divided rotates like a right-handed screw entering an object (what I have described as rotation to the side of the lesion). This point is of further interest when we remember that intracranial section of the auditory nerve was responsible for rotation in exactly the same direction as that in which the animal rotates when one of the inferior peduncles of the cerebellum is divided; that is to say with a left-sided lesion in both cases the animal rotates like a right-handed screw entering an object.

That the bulk of the afferent impulses, whose interruption are responsible for this phenomenon, reach the cerebellum by way of the auditory nerve and the inferior cerebellar peduncle is evident from the above considerations, but that all of the impulses do not reach the peduncle from the auditory nerve is made clear by the fact that lateral section of the medulla below the auditory nerve and its nucleus sometimes results in similar rotation of the animal about its longitudinal axis. And although such rotation does not always result from this lesion, yet the other indications of disturbance of equilibration are the same when these tracts are interrupted far back in the medulla as when the inferior peduncle is itself divided close to the cerebellum.

At first sight the disorders of motility would appear to lend strong support to the view that the cerebellum has a downward action on the muscles of the limbs through the spinal centres, but that such a conclusion is open to serious question is evident from a consideration of the results obtained by Claude Bernard* in frogs and puppies, and by Mott and Sherrington† in monkeys, for these observers found that impairment of movement in a limb resulted on section of the sensory roots of the spinal nerves supplying the limb.

If the interruption of afferent impulses in their passage through the sensory nerve roots is capable of producing impairment of movement, there is no reason why the interruption of similar afferent impulses passing up the lateral region by the medulla and in the inferior cerebellar peduncle should not be also capable of bringing about a similar result.

That this is probably the correct explanation of the way in which defective movement is brought about by division of one inferior peduncle or by lateral section of the medulla is suggested by the fact that the degree of sensory and motor impairment in the limbs is very much alike, that is, the limb in which motor power is most defective after these lesions is that in which most sensory impairment was met with, while that in which there was least sensory impairment was that in which there was least defect of movement. It is further significant, in this connection, that improvement

* Claude Bernard, "Leçons sur la Physiologie et la Pathologie du Système Nerveux."

† Mott and Sherrington, 'Roy. Soc. Proc.' 1894–5, Vol. 57, p. 481.

in sensory conduction could always be detected before there was any sign of improvement in motor power in these animals.

If the above is the true explanation of the way in which motor paresis is brought about by lateral section of the medulla or division of the inferior cerebellar peduncle, these results, taken in conjunction with those in which the posterior columns and their nuclei were divided, make it probable that the path of the afferent impulses whose interruption in the sensory roots is capable of causing impairment of movement is by way of the direct cerebellar tract rather than by the posterior columns.

That the cutting-off of some afferent impulse is responsible for the ocular displacements seems clear. It is interesting to note that such impulses appear to have two paths from the periphery, in that interruption of both the direct cerebellar tract and the posterior columns results in ocular displacements, though in the former case, as in division of the inferior peduncle of the cerebellum, the eyes are displaced away from the side of the lesion, with the displacement most marked in the opposite eye, while in the latter case the eyes are displaced to the side of the lesion, the displacement being most marked in the eye on that side.

It is curious that the ocular displacements which result from section of the inferior cerebellar peduncle should differ so widely from those which follow section of the auditory nerve, after which lesion the eye on the same side rotates downwards and inwards (towards the opposite side), or sometimes outwards (to the side of the lesion), while the opposite eye, in which there is most displacement, and which rotates downward and outward after section of the peduncle, in the case of the auditory nerve turns inward, and, according to Bechterew,* also upward.

The fact that the direction of displacement of the globes which results from section of one inferior peduncle of the cerebellum, is the same as that which results from ablation of one lateral half of the cerebellum, opens up the question as to whether the latter displacement is not also an indirect effect rather than one due to the taking-off of a direct influence normally exerted on the ocular muscles by the cerebellum.

With regard to nystagmus, nothing need be added here to what was said in my former paper.†

The spasm which was so easily detected in the back and neck muscles on the side of the lesion alone furnishes us with any satisfactory information with regard to the possible control which the cerebellum may exert on the spinal centres, an action which seemed highly probable from the results which were met with after ablation of one lateral half of the cerebellum. No reliable conclusion can be arrived at in connection with the spasm in the limbs, which was not of the very pronounced character such as was met with after cerebellar ablation, and which, therefore, was difficult to distinguish from voluntary contraction of the muscles by the animal.

* Bechterew, 'Pflüger's Archiv,' 1883, Vol. 30, p. 312.

† *Loc. cit.*

More disappointing still was the absence of evidence from the state of the tendon reflexes, for from their condition of exaltation after ablation of the cerebellum, it seemed likely that they would furnish still more definite information with regard to the question of control of the cerebellar over the spinal centres, when the inferior cerebellar peduncle was divided on one side; instead of which anything approaching the degree of exaltation of the tendon reflexes met with in the former experiments was never observed, and while the evidence on the whole pointed to the knee-jerk on the side of the lesion being slightly more increased than that on the opposite side, this was a question about which there was always a good deal of doubt.

While the state of the reflexes furnishes no satisfactory evidence in support of the view that the cerebellum exerts a control over spinal centres, the reflexes certainly do not supply any evidence to strengthen the view that this organ reinforces the spinal centres, for in no instances was there any diminution, much less abolition, of the tendon reflexes after section of one inferior cerebellar peduncle.

The blunting of sensibility met with is further proof that the cerebellum is concerned with sensory as well as motor processes, as was contended in my former paper. It is also important to find that the distribution of the sensory impairment after section of the inferior peduncle is the same as after ablation of one lateral half of the cerebellum.

Important as are many of the results that have already been discussed, none are more important, and few as interesting as those obtained on comparing the electrical excitability of the two cerebral hemispheres after section of one inferior peduncle, or after partial hemisection of the medulla. From the increased excitability of the cortex of the opposite cerebral hemisphere met with after ablation of one lateral half of the cerebellum, I concluded that the one half of the cerebellum normally exercised a control on the opposite cerebral cortex; it is therefore gratifying to find this view further supported by the results now under discussion. The fact that with all the cerebellar centres intact, and with the paths by which impulses may pass to the cerebral hemispheres also intact, section of one inferier peduncle of the cerebellum is followed by a lesser degree of excitability of the cortex of the opposite cerebral hemisphere, as compared with that of the hemisphere on the same side, suggests the possibility that the influence of control exerted on the opposite cortex by the half of the cerebellum whose inferior peduncle is divided, is heightened by the taking-off of some afferent inhibiting influence, normally acting on this half of the cerebellum, and reaching it by way of the inferior peduncle.

This view is strengthened by the remarkable results obtained by the intravenous injection of absinthe in animals in whom the same lesions had been previously produced. That with the pyramidal system absolutely intact from the cortex to the spinal centres, and that with the path from these to the muscles of the fore-limb on the side of the divided cerebellar peduncle also intact, there should be an entire absence of contraction of the muscles of this fore-limb, at a time when all the other

muscles of the animal are engaged in the general convulsions, induced by the drug, seems hardly credible, but is nevertheless the case. The only ways in which such an effect could be accounted for are, either by supposing that in order to reach the muscles of the limb in question the epileptic spasms generated in the cerebral cortex have to pass through the cerebellum to reach the spinal centres by way of the inferior cerebellar peduncle, which being divided prevents the impulses from passing; or we must admit that some afferent inhibiting influence has been taken off the half of the cerebellum whose inferior peduncle has been divided, and that this allows this half of the cerebellum to exert an influence on the opposite cerebral cortex sufficiently inhibitory in character to prevent the centres from being discharged by the absinthe. From what we know of the way in which impulses are conducted from the cerebral cortex to the periphery, there seems little likelihood that the former of these explanations is the correct one; while the evidence at our disposal on this point makes it probable that the latter is the correct explanation of the mode of production of the phenomena under consideration.

That the muscles of the posterior extremity on the side of the lesion contract, though less powerfully than do those of the opposite limb, is evidence that the same degree of control is not exerted on all the centres of the opposite cortex; but it is also possible that some of the spasm in the muscles of the posterior extremity on the side of the lesion may originate in the cerebral cortex of the same side as the limb.

The way in which the convulsions are diminished, and tonus largely replaces clonus during the muscular contractions which take place in the anterior extremity on the side on which the posterior columns and their nuclei have been divided, are interesting points, as is the fact that these differences become more pronounced after a series of convulsions; but in dealing with so much that is unfamiliar, it appears to me to be better to record the facts without at present entering into any speculations as to their significance.

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