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RESEARCHES

ON THE

PHYSIOLOGY OF THE CEREBELLUM.

By S. WEIR MITCHELL, M.D.,

MEMBER OF THE NATIONAL ACADEMY OF SCIENCES.[1]

During the last six years I have at various times engaged in studying the difficult subject of the physiology of the cerebellum. Like most observers, my experiments have been made chiefly, but not altogether, upon birds, for the reason that these alone survive the ablation of the organ in question. I have gradually reached certain general conclusions as to the cerebellar ganglia, which differ from commonly received opinions, while as regards birds I shall be able to make probable a theory which in connection with some of my former researches must, I think, modify very considerably our notions in regard to the spinal and cerebellar functions of this important class. In order to clear the ground for the reception of my own theories of cerebellar activity, it will be necessary in the first place to examine briefly the older conceptions, a task rendered the more easy by the prevalent dissatisfaction with which they are regarded by most living physiologists. The foundation for my own opinions must rest upon experimental and other proofs peculiar to my personal researches, and also upon a wide general consideration and critical study of the clinical history of cerebellar disease. There are at present but two theories of cerebellar function which hold any place in the esteem of physiologists. The most popular until a few years ago was the conception which grew out of Flourens' researches, and which was due to that great observer. He held, as is well known, that the cerebellum is the sole organ in which are co-ordinated the muscular movements of the body. Every year has thrown increasing doubt upon this view, against which he himself furnished unanswerable arguments by showing that birds occasionally recover from the

[1] The conclusions of this paper were communicated to the Biol. and Micr. Dept. Phila. Acad. Nat. Sci., Jan 18, 1869.

loss of the cerebellum, and in time have restored to them the co-ordinating power which for a period after the operation appears to be in abeyance. My friend, Prof. Dalton, has been equally fortunate in saving some of the subjects of his ablations of the cerebellum, and in seeing them regain entirely the functions supposed to depend upon its existence. The birds similarly studied by Lussana he describes as never recovering entirely their ability to use the muscles with certainty, but Dr. Dalton's observations are too absolute to admit of doubt, and, as we shall see, he is fully sustained by my own experiments. Moreover it has been repeatedly shown that in locomotor ataxia, a spinal malady, the co-ordinating power is remarkably affected. It is quite needless, however, to urge further these or other arguments, and they are many, against the view of Flourens. It is enough that clinical experience is against it, and that after loss of the cerebellum, the rare survivors of the operation resume in time the function supposed to be forever abolished with the destruction of the ganglion in question. The explanation of the undoubted disturbances of muscular action, which are seen immediately after cerebellar ablation, will occupy us at another place.

Certain modified forms of the opinion held by Flourens have been entertained from time to time by other observers. Thus Bouillaud regarded the cerebellum as the centre which presides over equilibration, and allotted to the cerebellum the co-ordination of the movements of the eyes, speech, and mastication, rejecting the notion which relates this organ to the instinct of propagation. The first part of his theory is more in accordance with facts than that of Flourens, but must be set aside upon the inexorable evidence afforded by the loss of the organ and the sequent symptoms.

Serres assigned to the middle lobe the function of excitor of the generative organs, and to the cerebellar hemispheres that of exciting motion in the members.

Wagner, at the close of an elaborate memoir, concluded, 1st. That the cerebellum is an organ exclusively motor for the muscular apparatus of animal life, and probably for that of organic life. 2d. That it has an essential share in the co-ordination of the symmetrical movements of the body, and notably in those of progression, while at the same time it cannot be regarded simply as a regulator of motion. 3d. That it may become the power of departure of a direct excitation (not reflex) of certain muscular apparatuses of organic life, particularly of the abdominal viscera, and especially of the genital organs, and probably of the heart. The first conclusion as to its exclusive motor function may at present be taken for granted; the definition of the method of interference (co-ordination) may be set aside as we have shown, and the last conclusion may be left to be dealt with when we consider the result of irritations of the cerebellum, only adding that with Brown-Séquard, I am of opinion that the relations of this organ to the apparatus of organic life require to be thoroughly

re-examined. The last physiologist mentioned reaches as yet only negative conclusions, nor am I aware that he has anywhere expressed himself definitely as regards the absolute functions of the cerebellum. Still more recently M. Vulpian, one of the best experimentalists of the day, has confessed, like Schiff, his inability to assign to the organ any positive function, while he holds, with Flourens, as to the result of artificial lesions, and seems to consider, with Lussana, that deep lesions are never followed by recovery of function and perfect natural motility.

As to the authors who have assigned sensory functions to the cerebellum, little need be said, since by general agreement they are held to be totally without support, save, perhaps, the single view advocated by Lussana and Dunn. These observers, especially the former, accepted the results of Flourens' classical experiments, but explained them by the supposition that the cerebellum is the ganglion of muscular sensibility. Such a view would be competent in explanation of the facts, but is antagonized by a large mass of clinical experience, and by the complete restoration of all motions after destruction of the organ, a fact which Lussana does not admit.

Magendie seems to have had a conception of cerebellar activity which assigned to it an office quite trivial as regards its great size, but which had too long possession of the books to be passed over in silence. He regarded the corpus striatum as having a backward propulsive energy, and the cerebellum as possessing a reverse activity, there being in health a physiological balance of control between the two, which was disturbed by the loss of either ganglion, so that the body was dominated by that which remained. In fact, mere puncture or irritation of the deep tissue of the cerebellum will often cause backward motion, the destruction of the organ not being essential to the production of this result. Besides which I have seen irritation of the medulla oblongata occasion it, and I have known superficial irritation of the back of the cerebellum to cause forward impulse, and irritation of the corpus striatum to occasion, though rarely, backward movement, so that Magendie's facts cannot be said to stand in undisputed simplicity.

Rolando held certain views in regard to the cerebellum which accord to some extent with my own. He held that it was, to use his phrase, an "electromoteur" in which was secreted a fluid destined to provoke muscular contraction. He adds, p. 417, that the cerebellum influences the intensity rather than the regularity of the muscular acts. I ought to add that as I have been unable to get his book, my quotations are at second-hand. Dr. J. Luys, in his excellent work on the nervous system, has given this view a larger development, and ably supported it chiefly by pathological evidence, to which I shall refer again. I do not know of any other author who has sustained this view by experimental arguments. I myself have for several years held and taught certain opinions which closely accord with

those I have last mentioned, and which it is the purpose of this paper to develop. To avoid all possibility of misconstruction, I quote the summary of Luy's[1] views with which he terminates the physiological part of his chapter on the cerebellum.

"Il peut donc être consideré comme une source d'innervation constante et provisoirement, comme l'appareil dispensateur universel de cette force nerveuse spéciale (sthénique) qui le dépense en quelque point que ce soit de l'économie, chaque fois qu'un effet moteur voluntaire ou involuntaire est produit."

From this condensed expression of his theory it will be seen that Dr. Luys regards the cerebellum, if I mistake not, as an apparatus for generating nerve force to be used according to the wants of the economy in the production of motor power, whether voluntary or involuntary.

The opinion which I myself entertain will be better understood at a more advanced stage of this essay, and I shall therefore defer its consideration.

The experiments which I have made upon the cerebellum have extended over portions of at least six years. That I do not speak without a very large experience may be gathered from the fact, that during this time I have ablated the cerebellum eighty-seven times, and performed more than two hundred and sixty experiments upon the influence of irritants on this and adjoining organs. Within the last year and a half, since I introduced into physiological investigation the use of extreme cold, made practicable by Richardson, I have added innumerable experiments to my older notes, and obtained results which, if not all that I could desire, are enough to tempt me to publish my conclusions.

Although it has been long recognized that, in studying the influence of injuries upon an organ, it is necessary to bear in mind the distinction between the phenomena due to loss of function, and those due to irritation, it appears to me that Brown-Séquard was the first to formularize this as a controlling law which should guide every physiological research. Its value in relation to experiments on the nervous system cannot be overstated, and had it not been too much neglected, there would have been far less confusion in regard to the symptoms which follow injuries of the organ we are about to study.

Bearing in mind the axiom above referred to, I desire, before proceeding further, to lay down certain rules of research, which should have a dominating influence in the present case, and which seem to me to cover the whole of the possibilities in the way of symptomatic phenomena.

1. When by disease or injury an organ is removed or destroyed, the process of destruction may give rise to irritations which react on distant organs, and occasion certain symptoms. These usually subside after a time, but where the injury to an organ is partial, and where any diseased process

[1] Récherches sur le Système Nerveux. Paris, 1865, p. 429.

continues, as a cicatrix, clot, or softening, they may become permanent. Examples of this will occur to the reader too readily to require illustration.

2. The loss of an organ may give occasion to, or permit forms of activity in other organs, which the healthy influence of this one controlled, as when the cutting off of cerebral influence allows of increased development of spinal reflex activities.

3. The loss of an organ exhibits itself in some manifest defect of function, or if after the stage of irritation is over there is manifestly no loss, then we are driven to the logical conclusion, either that the organ had no function, or else that the functional loss is provided for by a gradual increase of similar efficiency in some other organ, which alone becomes competent to the whole office, and during health must have shared with the lost part its peculiar duties.

I have caused irritation of the cerebellum in pigeons, rabbits, and guinea pigs, by the following processes: by inserting a strong needle-like awl through the skull; by injuring the organ after trephining, or, in birds, after slicing off a piece of skull; by injecting into the cerebellum globules of mercury with or without a minute amount of persalts of iron to arrest hemorrhage; by freezing the part more or less, and allowing it to thaw so as to cause congestion; and lastly, by painting the exposed part with tincture of cantharides or other irritant fluid. I shall pause here only to detail certain consequences which are either exceptional or unnoticed by former observers. The ordinary mechanical irritations need no special notice. Some of the results which follow other processes may be worth detailing. When in pigeons or mammals, I made a minute opening in the bone and injected with a syringe a globule of mercury into the centre of the cerebellum, it was usually followed by loss of steadiness of gait whenever the injection was deeply made, but if superficial the effects were slight or momentary, unless either the globule was very large, or the act was productive of hemorrhage; in either case death often ensued rapidly. In one case, that of a rabbit, I lodged a minute portion of mercury in the right side very profoundly. It gave rise to the longest continued *mouvement de manége* that I have ever witnessed. The animal rolled from the injured side, and unless guarded or supported, continued to do so during five weeks, when it began to acquire the power of walking without rolling, but was never able at any time during four months to move forward, all its locomotion being at first sideways and finally sideways and forwards. Then paralysis of both posterior limbs took place and was speedily followed by death. The site of the mercury was occupied by a clot surrounded by red softening, and the mercury had made its way downward to the base of the skull, and in spite of the most careful search, could not be found. In another case, the globule made its way forward and was found between the cerebrum and cerebellum. I presume that the great weight of the fluid used must be taken into account in explaining these facts.

I have already, in two papers, described very fully my own method of causing congestions by the use of Richardson's freezing spray, rhigolene being used in place of ether. The process has the one great objection of being difficult to limit, but is otherwise the only good method of causing profound congestion. Nothing in fact can be more perfect, as the whole part darkens visibly to the eye, vessels hitherto invisible appearing, and those which can be seen enlarging distinctly. The phenomena are probably from the beginning irritative in character, since the congestion follows instantly upon cessation of the spray, and goes on increasing in intensity as the part thaws, and the congestion spreads and becomes complete. So long as the freezing continues or is spreading, we may have suspension of function as complete as from ablation, but we shall hardly escape from some coincident irritation in the organ itself, or near ones at the extreme limiting edge of the chilled part. This objection applies alike to every mode of removing an organ or suppressing its function by local methods, while to none is there so little objection as to freezing, because as a rule the organ gradually returns to a state of health, and is not permanently injured. Sometimes the process employed occasions freezing of the medulla oblongata, when death at once occurs, as is also the case where for more than a moment the spinal cord is kept frozen in birds at any point above the dorsal vertebra. The results obtained by me from thus variously irritating the cerebellum or its pedunçles, differ little from those seen by former observers. Where I have had reason to differ from them in opinion, I shall speak most fully, and as briefly as possible on points where I am at one with them. The cerebellum of the bird seems to me less irritable to mechanical stimulus in its outer layers than that of rabbits, while I believe that in the guinea pig irritations nearer the surface are felt most remarkably. Simple mechanical injuries, needle wounds, etc., are very rarely fatal in birds or the mammals named, and occasion no lesions of special or general sensation. Contrary to Bernard's statement, I have not found digestion remarkably interrupted, nor have I seen any permanent intestinal troubles follow the operations. The motor functions alone suffer, and these are commonly re-established in their integrity within a period which varies from a few hours to ten days. As respects the form of these phenomena, consecutive to slight wounds, I have nothing to add to older knowledge. Superficial wounds, especially in birds, often occasion no visible symptom. Anteriorly and posteriorly deep irritations seemed to be felt as less profound ones are not, but although many authors have satisfied themselves that the animal then feels pain, I am not of opinion that this is certain. There is often a cry and a movement as the needle enters the deep posterior cerebellar regions, but apart from the difficulty of feeling sure that you have not disturbed the medulla, the movement may be due only to having entered a region which is an excitor of motion. Wounds of the deep lateral portions, involving the

origins of the middle cerebellar peduncles, cause the animal to roll around on his long axis and occasion, as do most deep cerebellar lesions, very notable squints, although these are apparently wanting in birds so treated. Any mechanical irritation which is deep enough to give obvious effects, is sure to produce disturbances of motility, either tendency to move or fall to one side, or else general want of balance with abruptness and jerkiness of movement—phenomena which to my eye read as though there were a combination of weakness with excitation of muscles, in some cases lateral, in others general, but as I have said, these by degrees disappear, the rolling passing into a tendency to walk in a circle before perfect recovery occurs. The torsion of the neck and spine noted by others I have also seen. Quite as often in grave wounds of the posterior regions in birds there was a drawing backward of the head so as to produce an appearance of strut in the gait.

The very singular backward movements due to certain cerebellar injuries have been seen by me in many cases of cerebellar wound, but are not capable of exact reproduction at will by this means.

Magendie states that irritation of the medulla oblongata may also cause retropulsion, and Longet and others are inclined to believe that it is always due to some effect of the injury to the cerebellum having reached this organ. Flourens states that superficial lesions of the former body cause forward motion, and deep injuries backward impulse. I have seen both caused in succession by one and the same lesion of the posterior part of the cerebellum. I am not myself of opinion that the backward motions, especially in birds, are due to accidental injuries to the parts below the cerebellum, or, at least, I am sure, not only that certain irritations, such as cold limited to the cerebellum, are competent to this effect, but also, I am sure, that in rabbits this agent applied moderately to the medulla oblongata through the occipito-atloid space, causes only general convulsions. In birds also, as I have shown, a large spinal region is competent to produce retropulsions. The forward impulse noted above also occurs sometimes after the application of cold to the cerebellum; but it is always the first movement, and looks like the wild effort of a confused animal at escape. It is promptly followed by retrogression, which has distinctly the appearance of an involuntary act, against which the animal struggles.

Brown-Séquard refers all the phenomena of this order to incidental mechanical interferences with the adjacent or subjacent parts, which he believes competent on irritation to occasion them. This might well be, and yet the cerebellum itself be also directly capable of producing, when injured, the same results.

The doubts which belong in this direction to mechanical injuries do not apply to congestions by the use of cold. The brain-case and skin being removed, a slight whiff of rhigolene, which barely freezes the superior and posterior cerebellar surface, causes backward motions, which cannot, I

think, be referred to the parts below when we remember how difficult it is in birds (even by prolonged use of the spray) to freeze deeply. Such being the case, if we admit the correctness of this experiment, we may at once conceive it probable that many of the results of mechanical injuries have a just right to be considered as truly due to the cerebellum. Apart from this, I feel with Ollivier and Leven that in some of mine, as in their observations, it was impossible that the means used could have mechanically disturbed other tissues.

I have occasionally seen brief vomiting follow deep freezing of the cerebellum, but I have rarely observed it after simple wounds of this organ.

The ocular nutritive changes described by many authors as due to cerebellar injuries, I have frequently met with in rabbits and in guinea pigs, but never in pigeons. The change consists in slight opacity of the cornea, usually on the side possessing the most violent squint; whether the fixity of the ball of the eye in these circumstances may not possess some influence in causing this condition, is, I think, a question of some interest.

As regards the graver lesion, amaurosis, Wagner believes that it is always due in pathological human cases to pressure on near organs, as the tubercula quadrigemina, but as high an authority, Brown-Séquard in his notes on Wagner's paper, states, that he has collected sixty cases of amaurosis of one or both eyes, in many of which there could have been no such affection of near organs. I have not seen this symptom in animals even where I have thrown foreign substances into the centre of the cerebellum to imitate clots, and where the animal has survived. Eleven cases lived after this treatment, but, although they exhibited more or less permanent lesions of motility and sometimes, though rarely, corneal troubles, I have met with no instance of loss of sight.

Certain other troubles, which follow ablation of the cerebellum, will be found referred to in their proper place.

Destruction of the cerebellum has been variously attempted, with a view to discover what functional deficiency follows its loss. The history of this portion of our subject has peculiar interest. Flourens, who removed the organ many times, inferred from the sequent symptoms of loss of equilibration that this was the co-ordinating centre, and the only one. In several instances, his animals recovered after loss of half the organ, which seems, however, to have awakened no suspicions on his part that his operation might have caused only irritative developments, which it was illogical to interpret as loss of function. In one case only does he report nearly total loss of the organ with recovery. He merely adds, that the cock lived more than four months and never regained his equilibrium, and this is the entire history there related.

Since then, several observers have ablated the cerebellum with intention to preserve alive the animal and observe the results. Longet failed in this

purpose, and states that his pigeons died in three days always, and his mammals much sooner.

That an experimenter so able should thus fail indicates the extreme difficulty of the task, in which, however, Renzi in 1858, and my friend Prof. Dalton, in 1867, were more fortunate. The latter kept alive four pigeons, which had lost large portions of the cerebellum. His last case is the best, because there seems to have been destruction of considerably more than half of this organ. There was nearly perfect co-ordination at the ninth day when the bird was killed.

Wagner—1861—seems to have been ignorant of Dalton's results, and strangely enough of Flourens, since he states that no one has hitherto succeeded in preserving alive animals which have lost the cerebellum. Examining carefully his results, it seems that he nowhere claims to have succeeded in removing more than two-thirds by weight of the ganglion in question; but he states that complete atrophy of the organ sometimes followed, which accords with Dalton's opinion, who has shown that the white substance below the line of incision undergoes profound textural alterations. In Wagner's cases there was final and complete recovery of co-ordinative power. Lussana—1862—also obtained recoveries, but describes the animal as incompletely possessed of the power to direct its motions. The organ is said to have been annihilated. All of these authors believe that, in these cases, the cerebellum was in certain instances thoroughly destroyed. All of them describe the immediate results as want of power to use the muscles usefully, loss of equilibrium, and the like. All of them tell us of the complete restoration of these lost powers, except in the case of Lussana, last quoted. Dalton distinctly affirms that there remained only some general feebleness, which accords with the statements of Ollivier and Leven, in describing grave lesions without ablation.

With this preface, I pass to the relation of my own instances of success in preserving pigeons alive after removing large portions of the cerebellum. I have been so fortunate, at different times, as to keep alive nine pigeons, from which large portions of the cerebellum had been taken away. One of these birds is now alive in my possession. In four, which were killed from two weeks to two months after the ablation, there was a destruction of the organ which I may call complete, since, although I had removed only one-half in three of them, the remainder was yellow, presented but few nerve cells or fibres, and contained in two numerous needle-like crystals of a pale brown colour. In the fourth I took away fully two-thirds of the part at first. In 1866 I preserved alive one pigeon after loss of half the cerebellum. It recovered entirely, but died suddenly at the thirty-fifth day. The remnant of the cerebellum was only partially disorganized, a portion at the back and left side appearing healthy. In 1868, the present year, one pigeon lived for three weeks, surviving all loss of co-ordination, except a certain awkwardness in using the beak. No. 7 of my series was

operated upon June 18th, and died August 4th, 1868. In this instance the pigeon was subject throughout to fits of convulsive gyration, alternating with stupor. Notwithstanding these, the co-ordinating power improved materially until a week from death, when the convulsions became violent and frequent. I found a large clot on and over the relic of the cerebellum, and much softening of the posterior cerebral tissues. The 8th pigeon was operated upon July 18th, 1868. I made a left lateral incision, removing a slice of bone, but respecting the central line, so as to preserve the longitudinal sinus. Fully half of the cerebellum was scooped out, and then with a two-edged knife I broke up a much larger portion of tissue. The bleeding was considerable. The usual symptoms appeared. On the 20th the bird was better, but incapable of standing or flying. On July 26th my assistant, Mr. Landis, took the bird to the country, and there carefully watched it. The remaining notes are his:—

Arrived at Chestnut Hill July, 1868.

July 26. In same state as on arrival—utter want of co-ordination—strikingly and amusingly manifest when it attempts to eat. Strikes at the grain of corn four or five times, missing it sometimes by several inches—then looks up at bystander as if ashamed of its awkwardness. Generally stands still with head drawn down and backwards, often making a noise akin to a grunt. When he moves about it is generally by a shuffling movement.

28*th*. After a few grains of corn (by hand) he was let down, and almost immediately had several *well-marked and characteristic backward movements*. Then crouched with breast on ground for a short time, when he arose and fed himself as on July 26th. From back part of wound on the head comes a watery fluid, showing under the microscope crystals. Was taken into the open air and sun for a short time, and flew a short distance. Is apparently strong, and his walk is improving.

August 2. Breathing somewhat oppressed.

7*th*. Walks quite well. *Can* fly, but does not often exercise this power. Is still awkward in feeding.

13*th* and 15*th*. Changed for the worse. Cause[1]—thermometer ranging from 65° to 57°.

17*th*. Better. Some want of co-ordination when making violent efforts, as running fast, &c.

22*d*. Apparently entirely well; but a slight pressure on occiput will cause a temporary return to former condition. Flies perfectly well.

28*th*. Found dead with wound in neck—caused by cat or rats.

No. 9 was operated upon September 8th, 1868. A left lateral incision was made so as to avoid wounding the cerebral sinus. The piece of skull was lifted, leaving it attached at one edge by soft tissues, as the lid of a box is by its hinges. When bleeding ceased I replaced this slice of bone, which became firmly fastened, so that no loss of tissue took place. Half of the organ was scooped out and more destroyed by the free use of the

[1] Sudden fall of temperature seemed to me very often to bring about a fatal result after ablation.—S. W. M.

knife, so much so that I had hardly a hope of the pigeon's living. Violent backward somersaults followed, and when in an hour these were over, there was feebleness and utter loss of power to effect any useful movement. Mr. Landis kindly took charge of this bird, and by great care succeeded in saving it. At the 18th day it was able to eat and drink, and could fly at the 30th day. At this date, January 15, 1869, it is in no respect different from its fellows, except that when pursued about the room it gives out sooner than others, and often quite suddenly, a symptom which exists in many of these cases, but which has a more peculiar value the further off in time it is seen from the date of operation. The latest sign of awkwardness was in a certain want of power to direct its beak. This Lussana also describes; and it is the slight and almost the only ground for his decision, that inco-ordination is permanent after ablation. It is possible that this difficulty may be due to a relic of the early motor troubles which affect the neck with some form of spasm, and which were remarkably conspicuous in the present case.

Before speaking more fully of the symptoms which follow ablations, it will be fitting to say something as to the precautions needed to insure even a rare and occasional success. As it has been objected by Schiff and others that the cerebral circulation must be greatly damaged by removing the cerebellum, I have, in some cases, made only a lateral or bilateral incision, slicing off the skull with a knife, and leaving a central bridge of bone, beneath which lay undisturbed the long sinus. In operating on the middle line, it is impossible to avoid dividing this vessel; so that death from hemorrhage is common. I have tried to avoid this result by the use of little clamps, actual cautery, etc., but have rarely succeeded. Practically, the pigeons which survived this method of attack presented no features of essential difference from those otherwise treated, so that in this matter the theoretical objection has no value. As convulsions of some kind always ensue, death from exhaustion is the next danger. This is avoided by swathing the bird in a bandage until able to stand, or until the fits are over. These are renewed very often by anything which causes sudden motion or struggle—as a loud noise, or the act of feeding artificially. It is best to operate when the bird has been lightly fed; and, of course, for some time the subsequent nourishment must be given grain by grain with the hand. As to this there is no trouble, since the power to swallow is undisturbed. Even on the first day the bird will usually drink of itself if the beak be put in water.

In Cases 8th and 9th I merely lifted the flap of bone, leaving it attached at one edge. When bleeding ceased, I replaced it, drawing over it the skin. Perfect union followed without loss of tissue. Usually no attention was paid to the wounds, which closed by membrane.

Consequences of Ablation.—Those which are immediate have been so well and so often described by abler pens than mine, that I shall be as brief as possible. Always, if the wound be a deep one, there are convulsions

which have a character of lateral or backward activity. With these, which soon intermit, we have a confusion of movement which is quite indescribable, and lasts much longer. It has usually been described by authors as a pure ataxy, without loss of power—a want of ability to group together the various sets of muscles so as to effect distinct actions like walking or flying. The animal staggers, falls this way and that, beats the air fruitlessly with its wings, lifts one leg or the other, and, in a word, exhibits what is truly described as an apparent want of co-ordination.[1] This is one way of reading the phenomena before us. There is, I think, yet another. If we conceive, as we have every right of evidence to do, that the cerebellum is in some kind of relation with nearly all the voluntary muscles of the body, we can see how an irritation which embraces in one plane all of the nerve fibres may give rise to irregular muscular motions, whose persistence will be limited only by the length of time during which the irritation continues. It is clear that nothing is more likely than that we shall have elicited a confusion of muscular replies, which, for a time, will interfere absolutely with the usually dominating influence of the volitional centres.

Ablation of the cerebellum is therefore equivalent, for a time, to extensive irritation of the organ, so that we have a graver reproduction of the symptoms which follow mechanical injuries, and which are severe in proportion as we incise the deeper parts of the organ. As we recede from the time of the operation these evidences of irritant action subside, until they are reduced to a minimum, or disappear altogether in the rare cases which survive the primary results of so terrible a traumatic lesion.

It is worthy of notice that during recovery the disorders due to irritation are often reproducible by noises, alarm, or rough handling—by any cause, in a word, which gives rise to abrupt movements or excited circulation. Under such circumstances the pigeon has some disorder of movement for a few moments, or at the beginning of a train of movements. Presently, however, this subsides, and the co-ordination is perfect again. The only permanent change which I have seen in pigeons is one, as to which I am personally quite confident, but which does not admit of absolute demonstration. All of the birds which have survived a long time seemed to me to be incapable of as prolonged exertion as their uninjured fellows, and to become tired far more readily. This point has more im-

[1] Flourens has noticed the likeness between alcoholic toxication and cerebellar loss. In the early stages of drunkenness in birds, there is, he says, a perfect concord of symptoms with those seen immediately after ablation of the cerebellum; whence he concludes that alcohol acts on this organ, but finally affects the ganglia of sensation and intellectuation. (*Rich. Exp. sur le Syst. Nerv.*, p. 401.)

It is, perhaps, hardly worth while to add, that I have found alcohol to cause in birds deprived of half or more of the cerebellum exactly the same symptoms as it does in uninjured birds.

portance than it would seem at first to have, as it bears somewhat upon the ideas which I shall develop as to the function of the normal cere bellum.

Some of the symptoms which follow ablation may be considered here.

Vomiting is not rare, but I have not seen it later than the second day, and it is curious to note that it followed only one case of those which outlived the operation a week. This fact alone would incline me to suspect that it is always due, when it does occur, to injury of the sub-cerebellar regions. I have already mentioned that digestion does not seem to suffer in lesser irritation of the cerebellum; neither does it remarkably, I may add, after ablation of that organ. Corn placed in the crop leaves it in the usual time, and the birds emaciate less than would seem probable, considering the primary loss of blood, the confinement, and the artificial feeding. None of these, however, account fully, to my mind, for the singular diarrhœa which follows ablation, and persists for a week or two.

If we admit the constant interference of the cerebellum in the motor activity of the muscular fibre of organic life, we may conclude that the diarrhœa is due to a succession of irritations affecting the motor tissues of the alimentary canal; but it should also be remembered that both Wagner and the author have seen loose evacuations as a result of cerebral ablations. Moreover, it is not yet clear whether the watery discharges in question owe their character to alteration of the intestinal or the renal excretions, both being discharged from a common cloaca.

The negative signs which follow recovery are also of interest; excepting some want of power to prolong exertion, there is left no locomotor defect. In the region of sensation no alteration may be perceived, and in the sphere of emotional activities I have been unable to detect any change, as the pigeons bill and coo, and do fierce battle like their healthy fellows. The question as to the influence of the cerebellum upon the generative organs has been pretty fully answered in a negative direction. I have no new facts to add to those of Wagner, Flourens, and Lussana.

The relation of the cerebellum to the generative organs is naturally connected with an influence which many suppose it to have over reflex movements, and especially over those which belong to the muscles of organic life. Brown-Séquard thinks, very properly, that it is necessary in this matter to repeat these experiments, attentive to the fact that impeded respiration, as he has shown, is apt to give rise to vigorous motions in the intestines, womb, etc. Now, in pigeons, such researches will be likely to have this element of doubt thrown in, because it is very difficult to open the belly without injury to the air-sacs, and consequent defect of aëration. Even in rabbits or guinea pigs, large opening of the abdomen disturbs breathing by taking away from the diaphragm some of the normal elastic pressure of the intestines, which aids the upward movements, so that, although it seems easy to expose the intestines, etc., and then irritating

the cerebellum to see if they move, it is by no means always possible to affirm that the sequent motion was truly a muscular reply to the cerebellar injury, and to this alone.

Bouilland and others have assured themselves that many at least of the partly reflex acts are undisturbed. To these belong deglutition and respiration, the influence of the loss of the cerebellum upon the circulation being still in doubt.

I have reserved to this time a review of the very important results obtained by the application of intense cold with Richardson's spray producer. At the risk of being tedious I shall venture to recapitulate the conclusions of my former papers, and the modifications which they have undergone.

During the spring and summer of 1867 I discovered that when the spine of birds (pigeons) is chilled anywhere above the dorsal vertebræ certain results follow; if the freezing be perfect and prolonged so as to act through the spine, death from asphyxia occurs just as if the spine were divided. This is due to the fact that the respiratory nerves come off all through this region, and is in accordance with older knowledge. Slight freezing causes gasping respiration, and great confusion of general motion, a hurried rush forward, sometimes general convulsions, with violent backward somersaults, and finally spells of curious retropulsion, alternating with stupors, and like all the former symptoms, less violent after chill of the lower cervical vertebræ than from like injury of the upper region. The experiments vary a good deal, but in many the wild confusion of movement and the loss of equilibrium with the apparent retention of a large share of usual power, all brought to my mind the cerebellar lesions I had so often seen followed by like phenomena. I also found that freezing of the cerebellum gave me precisely the same effects. I next discovered that direct irritation of the cervical spinal cord with irritants (capsicum) occasioned the backward spells after some hours, and the influence of the irritants proved more permanent than that of cold. At first I hoped to destroy for a time by freezing the influence of the cerebellar ganglion, but it is now clear to me that all the phenomena of action are due to the congestion which cold secondarily occasions, for it is impossible accurately to preserve the limits of the freezing, and so in the cerebellum we shall have a plane of varying congestion at the far line of the congelation. Also both here and in the spine, the motor phenomena are often delayed for a minute or more and then go on increasing in severity for a time. All of this is explicable if we comprehend that even while the freezing lasts there is probably a plane of irritation at the edge, that this speedily widens when we stop the spray, and that it quickly pursues the retiring line of cold as the re-established circulation passes by degrees into a congestion so profound as often to cause minute apoplectic effusions. Very little, then, of the convulsive acts is due to the direct effect of cold, much more to the intense and

overpowering congestion which in turn wears off. The added proof lies in the fact that local irritants which congest more slowly, occasion in the spine the same phenomena after the lapse of a longer interval.

In the following summer I made the more curious discovery, that cold applied suddenly to definite tracts of skin in pigeons gave rise to precisely the same retrogressive movements as if I had frozen the correspondent spinal regions. More strange still, when I froze the left or right side of the crop, the pigeon walked to the side opposite to that frozen. All of these movements followed the freezing at intervals as long as five to ten minutes, and sometimes failed altogether. Here, then, was a resemblance to the facts of cerebellar lesions which was certainly calculated to startle the modern physiologist. I should perhaps state at this point that all of the phenomena in question have been verified by Dr. Richardson and others.

Up to the last summer, that of 1868, the only time of the year when my daily business permits me to pursue physiology, I had referred all of the curious co-ordinated spasms, as well as the other appearances of loss of equilibrium, convulsions, etc., to the cerebellum. In June and July, however, I took up anew the question of cerebellar functions, and discovered to my surprise that after my pigeons had lost part or the whole of the cerebellum and recovered, they were still capable of exhibiting in perfection the retrogressive acts, backward convulsions, and lateral walking. Other irritants applied to the spine gave also the usual results, so that it became clear that I had been mistaken, and that the cerebellum was not needed to produce the phenomena I have described.

I made many efforts to irritate the lateral columns of the spine to cause lateral motion, but always failed to attain my purpose. If I could have kept alive a pigeon after dividing the spine in the neck, and then have frozen the portion below the section, I might have been successful in proving absolutely the independent possession by the spine of certain cerebellar properties. I endeavored to do this by keeping up artificial breathing after such sections, but was defeated by various obstacles which will occur to every biologist.

There is another fact which lies in the same direction as many of my own, and is of great interest in this connection. Brown-Séquard relates that when in the lumbar enlargement of the spinal cord of birds, he exposed to the air the gray matter which there lies externally, a curious disturbance of movement immediately followed, and was not observed elsewhere in the spine, at parts whose white neurine alone lies outside according to the common arrangement. The disturbance, he says, "very much resembles the so-called titubation, which exists after either the removal of the cerebellum, or the section of muscles of the posterior part of the neck." As I have shown, however, deep freezing higher up occasions the most

profound confusion of motion, because the congestion in this case reaches the gray matter easily.

In the light of all that I have previously pointed out, I shall now review the question of cerebellar function.

We must admit, in the first place, that apparent loss of co-ordination follows cerebellar lesions. It appears clear from my own researches, that these injuries do not cause this result, owing to mechanical and incidental affections of near parts.

In birds, injuries and congestion of the spine give rise, at first, to seeming in-coördination, or at least to exactly such phenomena as follow like injuries addressed to the cerebellum. When the cerebellum has been removed spinal irritation still continues to evolve the same symptoms as when the cerebellum exists untouched. These facts indicate for these two organs in birds at least, a curious community of pathological symptoms and probably of physiological function. If then there be such a functional entity having a separate seat as the so-called co-ordination, it belongs in birds to an extensive region, including the cerebellum and a large part of the spine.

There is yet possible, however, another view of cerebellar activity which will accept all of the facts and account for all. Let us suppose the cerebellum to be a great ganglionic mass, possessing the same motor functions as the gray matter of the spine, related like it, and through it, to the voluntary muscles. Irritations of its tissue, ablation, the temporary equivalent of extensive irritation, congestions, as from cold or other causes, might occasion both directly through the spine, or indirectly by reaction on its ganglia, just such confusion of motion, restlessness, and locomotor disorders, as we do actually see and as were said entitle it to be called the organ for co-ordinating muscular acts. As the irritation disappeared, so would the muscular disturbances, until, when there was no longer irritation, there would cease to be locomotor difficulties of the character described, the spinal centres having by degrees assumed with the aid of the will the function shared in health with the lost organ.

Referring anew to laws of research laid down at a former page, I remind the reader, that if an organ be lost, and no function *finally* disappears, it either had none or possessed one in common with some part which remains uninjured and capable of at last supplementing the function of the destroyed tissues. For these reasons I am disposed to deny to the cerebellum any larger share in co-ordination than exists in any ganglion employed in voluntary motion, and to assign to it a part closely relating it in powers to the chain of spinal ganglia. The cerebellum becomes for me, therefore, a great reinforcing organ, capable of being more or less used in volitional muscular motion. Its loss, as I have elsewhere stated, leaves finally no functional defect save some incapacity for prolonged motor activity.

The apparent in-coördination which follows section through the deeper

layers of the cerebellum, is simply a confusion of movement due to the joint action of two separate and interfering agencies. In health the cerebellum is called upon by the will when needed, and acts through the spine on the muscles. After irritation or ablation (the equivalent, for a time, of extensive irritation), we have two sets of forces in action—that arising from the excited and wounded efferent cerebellar fibres, a force inconstant, irregular, involuntary; and secondly, the normal activity of the will, which, in presence of the former disturbing power, fails to evolve the usual orderly reply from the muscles. The general result is seen in the strange confusion of movement which is so familiar to the physiologist.

I am very far from supposing that what I have here urged as experiment or argument is at all complete. I am well aware that much may be said against my views, and perhaps something more in their support. It is clear, however, that as yet we have had no cerebellar theory supported by any weight of experimentation. The theory which I have here set forth may or may not be correct, but it seems to me to have more in its favour than any other yet advanced. Should it meet with no success, it will still be impossible to frame any consistent hypothesis of cerebellar activity which does not account for the new facts in this connection which I have published; so that if these have been well and honestly observed and stated, I shall not have laboured altogether in vain.

I ought to add, that while I believe the cerebellum to be one of the great centres of force-development for voluntary, and perhaps involuntary motion, I am not at all prepared to assume that it has no other function. Whatever quarrel may be made with this argument as regards mammals, it seems to me quite clear that, in birds, a relationship of function with that of the spine is fairly made out, even if we hold to the older views of the co-ordinative powers of the cerebellum, a doctrine which I am quite indisposed to admit. While in birds, then, there is great reason to induce us to accept the view previously stated, and which would teach us to look upon the cerebellum as a great additional centre of motor power, called into habitual activity by the will, and co-operating with the spinal ganglia, there is nothing in experiments upon the cerebellum of mammals to contradict such a theory. Irritations of the cerebellum in this class occasion exactly the same kind of motor disturbances and irregularities as in birds. Ablation productive in mammals of primary symptoms in nowise unlike those of birds, ceases here to offer us further proof, because, as yet, no one has succeeded in saving the life of a mammal deprived of the cerebellum.

I ought also to add, that I have found it impossible to cause by cold addressed to the spine of mammals those phenomena which are seen in birds upon so disturbing either the spine or cerebellum. For this reason many will perhaps hesitate to admit in mammals that community of spinal and cerebellar functions which I have made at least not improbable in the class of birds. Nor would there be anything to shock us in such an admission,

because in the lower animals many functions are disseminated over large regions which in higher creatures are centralized, so to speak. This is well enough illustrated in the frog, which, after decapitation, executes many and complicated reflex acts with entire co-ordination, despite the absence of brain. There is therefore no doubt that the reptile class possesses, in a larger degree in the spinal regions, motor powers, which in higher classes exhibit themselves only under the influence of intra-cranial ganglia. The physiological gap between birds and their next higher neighbours in the ascending scale of life is a very wide one, so that if that were in a measure true of birds which proved not to be of mammals, it need excite no great surprise. I mentioned, early in this paper, that comparative anatomy gave us little aid in determining the cerebellar offices. On the other hand, comparative experiments upon animals below the class of birds, seem to afford important additions to the evidence already offered that the cerebellum is principally a motor ganglion supplementing the group of spinal nerve cells, and like them dominated by volition. I found it needless to experiment as to the cerebellum in frogs, fish, etc., since this had been already fully done. Thus, as Vulpian points out in frogs and fish, removal of the cerebellum alone produces no noticeable symptom, unless the peduncles have been injured. In these classes the organ is relatively small, and we may presume, if for a moment we accept my views, that the spine is largely predominant in the ordinary product of motor power, so that ablation of the cerebellum causes in these animals less than any that disturbance of movement which comes from irritating a vast number of motorial fibres.

It was at one time my intention to examine how far the pathological evidence in man would sustain the view of cerebellar function which I have, with many doubts, brought forward in the absence of any one more probable. After studying with critical care a large number of cases of cerebellar lesions, I found that very few of them could properly be used, owing to there having been no microscopical inspection of near organs. We have numerous symptoms, some of which at least we cannot reproduce by artificial injuries. They may be the legitimate offspring of the cerebellar disorder, but since they may also be due to affections of the medulla oblongata or optic ganglia, etc., we have no right to feel sure that these latter organs are not the true parents, unless they have been examined by every possible means. On the other hand, while many of the phenomena of disease are also seen in some modified shape in the laboratory, it is well to remember that, nearly always, disease acts slowly, giving us rarely those trenchant results which follow the abrupt interferences of the physiologist's scalpel. I may say, in conclusion, that after analyzing an hundred cases, Luys tells us that progressive muscular feebleness was noted in forty-five. I myself have reached nearly the same result from the study of cases other than his, and I feel at least authorized to say, that while

for reasons above stated the cerebellar pathological evidence is inconclusive, it is more in favour of the views I have set forth than of any of the precedent theories.

In conclusion, I desire to express my warmest thanks to my assistant, Mr. Landis, without whose ingenuity and care I certainly should not have been able to preserve alive any of the recent subjects of attempts at cerebellar ablation.