STUDIES ON THE MAINTENANCE OF THE EQUILIBRIUM OF MOTION AND ITS DISTURBANCES, SO-CALLED "FORCED MOVEMENTS." By L. J. J. MUSKENS. (Five Figures in Text.)

Reprinted from the Journal of Physiology.
Vol. XXXI. Nos. 3 & 4, June 30, 1904.

[*Reprinted from the Journal of Physiology.*
Vol. XXXI. Nos. 3 & 4, *June* 30, 1904.]

STUDIES ON THE MAINTENANCE OF THE EQUILIBRIUM OF MOTION AND ITS DISTURBANCES, SO-CALLED "FORCED MOVEMENTS." By L. J. J. MUSKENS, M.D., *Amsterdam, Holland.* (Five Figures in Text.)

EXPERIMENT has taught us that for vertebrates with horizontal posture we have to distinguish two principal types of forced movements in the strict sense, *i.e.* 1st, *rolling movement*, that is locomotion (rotation) in a plane, vertical to the longitudinal axis; 2nd, *circus movement*, locomotion in a circle in a horizontal plane, corresponding with the longitudinal axis of the body[1]. It is well to abandon the conception of some authors, who recognise two more forms of forced movement; clock-like movement and screw-like movement.

Repeated observations upon animals, from Selachians to Mammalians, lead to the conclusion, that the latter forms of locomotion are essentially circus and rolling movements under special conditions, viz. circus movements with a very short radius, and rolling movements, combined with a forward locomotion.

These two principal types of forced movements are either complete or partial. If complete, they manifest themselves in actual movements of rotation, nearly always interrupted by intervals of rest. During these intervals of rest, trunk, head and eyes are kept in a peculiar position which is characteristic for particular forced movements and corresponds with them. If incomplete, only a tendency to those forced movements is present, or only the characteristic position of trunk, head and eyes, or even a forced position of any one of these alone is found.

A further common characteristic of the forced movements and

[1] At present I will only mention a third type of forced movement, *i.e.* locomotion in a plane, vertical to both planes, mentioned above; a plane corresponding with the longitudinal axis of the body and vertical to the horizontal plane. In its complete form it is, perhaps, only met with after adequate lesions in invertebrates (arthropods); in its incomplete forms (falling backwards or forwards, with analogous phenomena in the motion of the eyeballs) it is met with in the higher vertebrates after lesions in the middle lobe of the cerebellum and the mesencephalon, also in some pathological cases.

allied phenomena after adequate lesions of the central nervous system is, that as a rule they are of a passing character, *i.e.* they tend to disappear or to become compensated. This holds good especially for the actual forced movements, which are often shortly after an adequate lesion very vehement, but less so for the forced positions.

As these last remain long after the actual movements have disappeared and often are present in lesions where no forced movements could be detected, the forced positions are to be studied at the same time.

Lastly, it must be pointed out as a characteristic of real forced movements, that paralysis of muscles or groups of muscles is not the cause, nor does it accompany any of the manifestations of the forced movements, although paralysis occasionally may be brought about by the lesion which has produced the latter.

To these forced movements, although they are common phenomena after any lesion of the cerebro-spinal axis, proximal to the exit of the eighth nerve, it seems to me, inadequate attention has been paid. Due observation of the phenomena observed in lower vertebrates (especially of the eyeballs) can throw light on the genesis of some similar phenomena met with in higher vertebrates. I will however point out from the start, that our knowledge of this question entirely acquired from lower cold-blooded vertebrates and mammals with horizontal posture cannot be applied without the severest criticism for beings with erect posture, as the system of nervous arrangements for the equilibrium of motion must have undergone some fundamental changes of its function when the locomotion in a plane, parallel with the longitudinal axis of the body, was given up for locomotion in a plane vertically placed to that axis. This becomes more evident, if one bears in mind that the two principal forms of forced movements, viz. rolling and circus movements, are practically identical in the case of the mammal with erect posture, that is, only different in radius of circular locomotion, whereas we saw, that in the large majority of the vertebrates these two forced movements are performed in planes vertical to each other.

My own work on this subject has been carried out along lines laid down by comparative physiology.

This mode of procedure, besides other advantages, enables one to separate the constant and fundamental phenomena from accidental ones, merely dependent from a special organisation, or from the medium in which the animal is living. It can be stated, with certainty, that the occurrence and predominance of any of the three principal forms of forced movements, *i.e.* rotating movements in the horizontal and in the two vertical planes, depend largely, if not solely, from the most customary mode of locomotion of the animal in question. These forms of locomotion are, I take it, firmly preformed and fixed in the physiological organisation of the nervous system. So we may expect, as far as the invertebrates are concerned, more easily to cause circus movements in the vertical plane, corresponding with the longitudinal axis of the body, in shrimps, which often in ordinary life make similar movements, than in land-living arthropods, which hardly ever do so; equally difficult we shall find it to elicit rolling movements in crabs, which, as is well known, hardly ever are inclined to make a similar rotatory movement spontaneously.

What follows is an account of experiments conducted along these lines; at the same time I cannot claim originality in the majority of the experiments.

Whereas most of my personal observations deal with vertebrates, a short account may be added of what I had recently the opportunity to see of forced movements in a class of animals, so profoundly differently organised as are the octopods. It may at least serve as a proof that wherever free locomotion occurs in the living nature forced movements are prone to occur.

The subject of forced movements has naturally very many points of contact with the so-called compensating movements of eyes, trunk and extremities. Some authors explain these forced movements as even caused by the sensation of dizziness counteracting them. Yet I think we can and must keep them physiologically quite apart. Also we have opportunity in the octopods to observe very complicated compensatory movements which have no relation whatever with real forced movements[1].

OCTOPODS.

These creatures perform two forms of locomotion. Firstly they will sit down quietly on the bottom of the tank and bring forward slowly their arms in such a way that the body moves slowly in the same direction. The eyeballs are constantly moved about reconnoitring the field. The lateral position of the eyes excludes a binocular visual field, so that the eyes move in complete independence. The other form of

[1] Compare *Engelmann's Archiv für Physiologie*, 1904, pp. 49—56.

movement is a rapidly shooting locomotion. It is caused by powerful rhythmic contractions of the mantle-clock. A natural result of this motion is that its direction is backward. The arms are carried in the rear in flaccid condition and as a slender body, head and eyes directed backward, the animal will shoot with great velocity against the glass wall of the tank.

The pupils of the octopods are oblong, and in all positions, whatever the locomotion may be, the position of these pupils remains the same, *i.e.* horizontal. Even in the extreme inclined position, especially if the head is bent forward, this holds good. Only after extirpation of the otolitic organ on one side this horizontal reflex will disappear on the side operated upon. As to their forced movements I observed them more or less frequently in all three planes. Especially frequently was seen rotation around the longitudinal axis of the body. Especially after extirpation of one otolitic organ (from the ventral side) the rotation takes place to the side of lesion. After this operation the arms of the animal, while sitting quiet or moving slowly forward, are sometimes placed in a spiral on the bottom of the tank.

Real constant circus movements I never observed, neither after one- nor after double-sided operation. Occasionally, however, I saw them occur after one- or double-sided severance of the otolitic organs. J. v. Uexküll[1] observed circus movements to the non-operated side after section of the posterior commissure; the author ascribes these movements to the curious curved position of the neck of the animal.

The *manège* movement in the vertical plane coinciding with the longitudinal axis of the animal is seen, as far as my observations go, only after double-sided severance of the otolitic organs.

Lower Vertebrates.

Some of the *Selachians* (Acanthias, Scyllium) for various reasons are certainly most useful for experimental work in this line. During a research work in the Zoological Station at Nieuwediep in 1893 my conclusions were:

1. Hemisection of the cerebro-spinal axis through the optic lobes (mesencephalon, homologon to the corpora quadrigemina of the higher vertebrates) constantly produced circus movements towards the *uninjured* side, with shorter or greater radius. This is quite in agreement with the results of Steiner[2].

[1] J. v. Uexküll. *Zeitschrift für Biologie*, 31, S. 584. 1894.

[2] J. Steiner. *Functionen des Central-Nervensystems.* II. Fische. Braunschweig, 1888.

2. Hemisection of the medulla oblongata, proximally to the exit of the 8th nerve, produced with the same constancy *rolling* movements towards the injured side[1].

It may be added, that in both cases the body of the animal (as well as its eyeballs) was kept also during rest in a forced position, corresponding with the mode of movement, *i.e.* in the first case the vertebral axis was bent, with the concavity to the unimpaired side; in the second case the trunk was kept more or less in a spiral, tail and dorsal fins deviated also correspondingly[2]. In both instances the movements were observed in individual cases for many days, till the animal died from confinement in the tank, and after death the forced position was to a certain degree kept up, due to an asymmetrical manifestation of the rigor mortis. I can add that by subsequent operations the possibility could be excluded, that either defective visual field or alteration of the eyesight, or altered innervation of the eye-muscles, caused by the operation, had anything to do with the resulting abnormality of locomotion.

Having realised the above essential phenomena I was struck by the relation which appeared to exist in these animals between rolling movement to the impaired side and circus movement to the unimpaired side. The rolling to the impaired side after hemisection of the upper part of the medulla oblongata was often interrupted by circus movements to the unimpaired side of short radius, and this was noticed to happen the more frequently the more proximally the hemisection was applied. On the other hand it was noted, that the animals operated upon the mesencephalon, and performing their circus movement to the healthy side, were usually bent over to the impaired side, *i.e.* if the animal was lying on the bottom of the tank, it rested not on its belly, but rather on its flank, corresponding to the side operated upon.

This position of the body, showing a tendency to roll to the impaired side, became the more marked the more distally the hemisection was performed, and actual rolling movements interrupted more and more the circus movement to the unimpaired side. It was further noted, that asymmetrical operation, proximal to the optic lobes, as well as operations upon the roof of the optic lobes, caused no such abnormalities of locomotion, and that faradic excitation of these proximal parts did

[1] To preclude misunderstanding it may be stated, that if the R(ight) side was operated upon, as was the case as a rule in my experiments, the sidewards locomotion, produced by the rolling, took place to the R. side of the animal, taken from its initial position.

[2] Compare J. Loeb, *Archiv für die Ges. Physiologie.* 1893.

not produce any motion of trunk, tail or fins, whereas excitation of the deeper layers of the mesencephalon produced vigorous kicks of the tail to the side stimulated and various movements of the eyeball of the same side[1]. Lastly, I noted that in embryos of Mustelus vulgaris and of different Ragidae of 2 cm. length and less, by pricking with a fine needle through the isthmic portion of the cerebro-spinal axis, similar results were obtained, the creature winding itself up as far as possible around its own umbilicus.

Numerous experiments in *frogs* have borne out the main facts pointed out above. After unilateral lesion (on the right) high up in the medulla oblongata (proximal to the point of exit of the VIIIth) the screw-like position of the body and limbs is very marked (Fig. 1); the left eyeball bulges, the right pupil is smaller, the right cornea reflex absent; the right foreleg is adducted, the left one abducted, the right hind leg is drawn up, the left one extended, the head is rotated along the longitudinal axis towards the right side[1] and also bent to the right side. All this is best observed if the animal is floating in water; the photograph (Fig. 1) is taken from above, the animal floating in

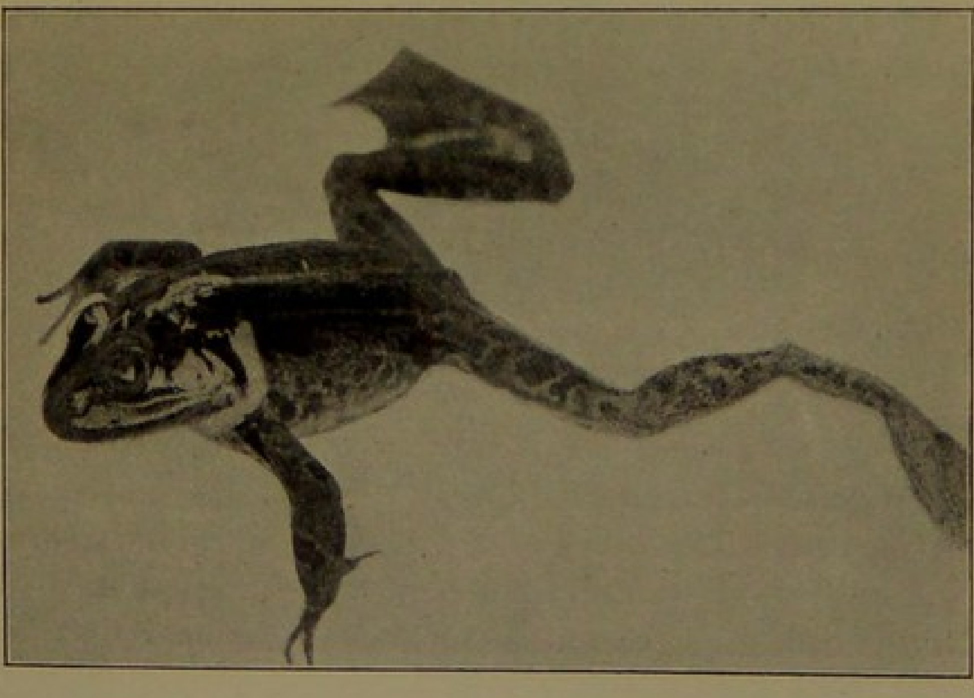

Fig. 1.

water. Here again it strikes the observer how nearly related are the two above-described forms of forced movements, rolling to the impaired

[1] Compare J. van Deen. *Nieuw Archief voor Binnen- en Buitenlandsche Geneeskunde in haar geheelen omvang*, 1ste Jaargang, 1848, p. 304. Compare Ferrier, *Functions of the Brain*, pp. 72—84.

side and circus to the unimpaired side. This combination manifests itself in the leaps these frogs will make after a few days; they will jump to the left and come down on the right flank. As a rule immediately after the lesion they perform rolling movements to the right with great vigour; this rolling becomes less marked after a while and is replaced by circus movements to the unimpaired left side, first with a smaller, later with a greater radius. Quite in accordance with what I noted above for the sharks, it was with great constancy observed that the more proximally the hemisection was performed (the base of the mesencephalon being the most proximal point), so much the more the circus movements to the unimpaired side prevailed. These frogs, also those which immediately after the lesion of the base of the optic lobe commence their circus movements and keep them up for many weeks, will keep their head bent over the impaired side, showing a tendency to roll to the right impaired side.

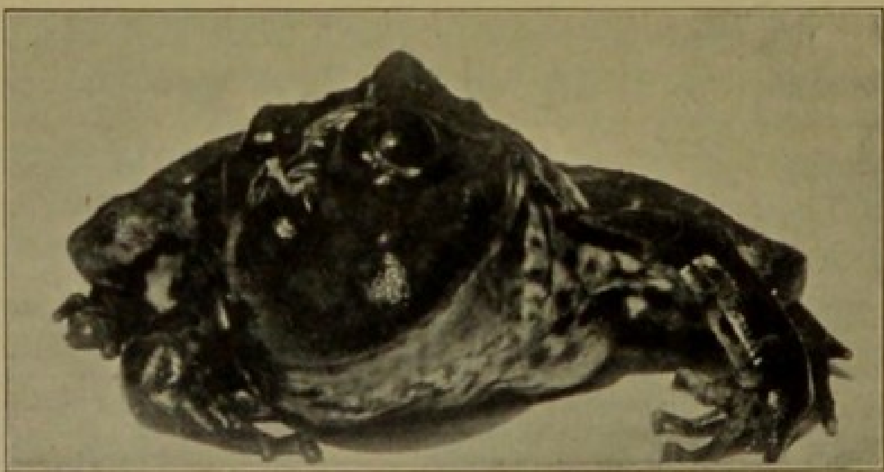

Fig. 2.

In frogs the forced movements are very persistent. In a good many cases the rigor mortis made its appearance in an asymmetrical way[1]; this phenomenon is however better studied in warm-blooded animals.

If we compare the results reached with frogs and sharks, we arrive at the conclusion, to which point also a number of experiments in various other lower vertebrates:—

1°. That rolling after unilateral lesion of the hind-brain, and circus

[1] Starting from the idea that simple forced movements and positions are due to a difference in the muscular tone on the two sides, or some other asymmetrical condition of tone in certain muscle groups, I cut in two specimens of Rana catesbeiana on one side all the posterior roots. In both cases very marked curvature was produced in the bodily axis, with the convexity to the side of the lesion, in one case also the head was rotated along the longitudinal axis to the side of the lesion.

movement after unilateral lesion of the base of the mid-brain, appear to be, in lower vertebrates, fundamental phenomena, especially localised in these parts.

2°. That rolling to the impaired side and circus movement to the non-impaired side are phenomena physiologically narrowly related.

3°. That in these experiments on the simple organised vertebrates there is no reason to believe in any diametrical opposition of forced movements of an irritating and of a paralysing nature—any more than we recognise a similar opposition after a lesion of the semicircular organs.

Rabbits and Cats.

Most of my observations on rabbits date back from some years ago, and what I shall have to say about them refers largely to phenomena seen after a puncture in the cerebellum, applied 2—3 mm. posterior and lateral to the external occipital protuberance, piercing the middle peduncle. The puncture was performed with a long steel needle, the animal being anæsthetised with ether; the needle was thrust vertically to the base of the skull, in a slightly forward direction. As to the observations in cats, they were made after various unilateral operations upon the cerebellum and its peduncles on Mr Horsley's suggestion. I found rabbits and cats also useful, from which I had extirpated the right flocculus in order to study the subsequent degeneration in the central organs. In both animals section of the middle peduncle

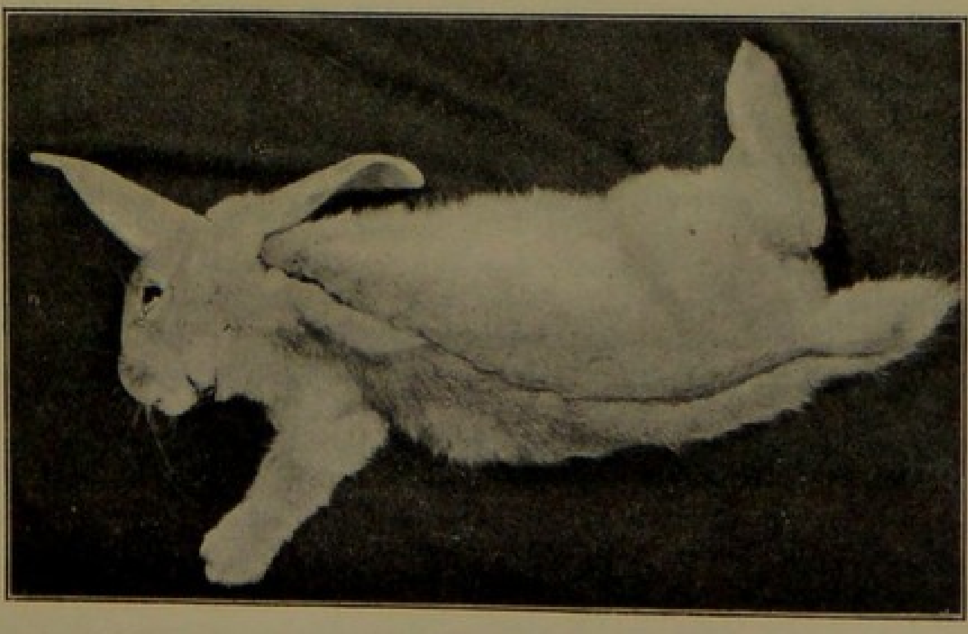

Fig. 3.

was the most effective in producing rolling movements. The rabbit is a very convenient animal in this line, on account of the vehemency of the forced movements and its free mobility of the eyeballs.

By all these procedures mostly rolling movements to the injured (right) side were produced, *i.e.* when the animal was placed on the floor the sideward locomotion took place to the right of the animal (Fig. 3), being in its primary position (like a right-handed screw, after the expression used by Risien Russell); especially so if the middle peduncle was injured. Whereas all the preceding observers make the same statement, as far as the rolling movements are concerned, the most astonishing discrepancies are found in the literature about the direction in which this takes place. The authors to whom I allude experimented upon the cerebellum, the peduncles and the pons. Longet[1], Lafargue[2], Friedberg[3], Leven and Ollivier[4], Luciani[5], and Russell[6], after ablation of a lateral lobe of the cerebellum in a dog, recorded rolling movements to the uninjured side, Magendie[7], Schiff[8] and Ferrier and Turner[9], and A. Thomas[10] to the injured side. If it be accepted, that the direction of rolling should be named after the side of the animal in its primary position, to which the sideward locomotion takes place, my results correspond with those of the last authors. In regard to this important point it appears to me that the discrepancies of these competent observers are largely due to: (1) Inadequate nomenclature of the resulting forced movements. Especially the French observers did not always distinguish the two types of rotation: *rolling* and *circus* movement, the word "rotation" being often used for both of them. (2) Incorrect description of the direction in which the rolling took place. To this source of error clinicians were particularly liable, as they were inclined to apply expressions, in use clinically, to phenomena observed in experiments. If an animal tends to roll to the right (*i.e.* sideward locomotion with regard to the primary position) the face will

[1] Longet. *Anatomie et Physiologie du système nerveux*, Paris, 1842, I. p. 735.

[2] Lafargue. *Thèse inaugurale.* Paris, 1838.

[3] H. Friedberg. *Virchow's Archiv*, XXII. p. 61. 1862.

[4] M. Leven and A. Ollivier. *Archives générales de Médecine*, 1862, p. 2, *et* XXV. p. 513. 1863.

[5] L. Luciani. *Das Kleinhirn*, 1893.

[6] J. S. R. Russell. *Phil. Trans.*, CLXXXV. p. 837. 1894.

[7] M. Magendie. *Journal de Physiol. expér.*, IV. p. 399, 1824, and *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, I. p. 265.

[8] M. Schiff. *Lehrbuch der Physiologie*, I. p. 354. 1858.

[9] D. Ferrier and A. Turner. *Phil. Trans. Royal Society*, CLXXXV. p. 726. 1894.

[10] A. Thomas. *Cervelet*, p. 325. 1897.

be turned to the left side, or, after Ferrier and Turner, there will be tilting of the chin to the left side, and some observers will call the actual rolling in that sense rolling to the left[1]. On the other hand many observers simply stating that the animal turned to the right neglected to point out whether this was meant from the standpoint of the animal or of the observer, as was already observed by Prevost[2]; in the last case, of course, it makes all the difference whether the observer stands in the back or in front of the animal.

After careful consideration and comparison of the work of authors, who worked in similar lines, I find that most statements agree with the general result obtained by me in numerous unilateral experiments on the cerebellum and its junctions with the cerebral axis in rabbits and a good many ones in cats.

A brief *résumé* of these results is as follows:

Unilateral lesions of the middle and upper cerebellar peduncle and unilateral (partial more than complete) removal of a lateral lobe of the cerebellum cause rolling movements to the side of the lesion, or at least tendency to it, *i.e.* forced position in the same sense (screw-like position). The most vehement rolling was observed both in the cat and in the rabbit after lesion or section of the middle peduncle and the tuberculum acusticum.

As to the unilateral lesions of the lateral lobe of the cerebellum it

[1] In Luciani's admirable work on the cerebellum (German translation, p. 88, 1893), some notes can be found which show how advisable it is to keep to one way of describing these phenomena, as accepted by me. The animal's head is turned so "that the L. ear is in a higher plane"; this animal, which turns "in the same direction," rolls to the L., according to Luciani, whereas it is surely to the R. that the locomotion takes place. Equally H. Friedberg's (*Virchow's Archiv*, XXII. p. 61, 1862) patient, in whom after death a hæmorrhage was found under the tentorium on the L. side, performed movements of rolling and circus to the diseased side, after Friedberg; after the above nomenclature the rolling was performed to the impaired, the circus to the intact side. R. Russell's mode of describing the direction of rolling, viz. after the direction of the movement of the upper quadrant (*British Medical Journal*, p. 909, 1897) is no doubt as correct as the way advised here (after the direction of the resulting locomotion), but is not as simple. Where we have to deal with rotation in man, it is my custom, as is also Russell's, to imagine the person in question in the all-four-position and name the direction after the usual way. P. Gratiolet and M. Leven (*Comptes rendus de l'Académie des Sciences*, 51, p. 17, 1860) state that Schiff and Cl. Bernard reconciled the difference in the alleged direction of the rotation after cerebellar lesions, in that they showed, that Lafargue and Longet (as later R. Russell) caused experimental lesions especially of the anterior fibres of the middle peduncle, Magendie of the posterior bundles. At any rate it appears probable, that a detail in the operative procedure is largely responsible.

[2] J. L. Prevost. *Gazette médicale de Paris*, p. 117, 1869.

must however be understood that neither vehemence nor the duration of these rolling movements is directly proportional to the extent of the lesion. A very good illustration of this was obtained in a series of three experiments I lately performed upon cats. In the first I removed only the ventral part of the flocculus, in the second the whole flocculus, in the third nearly the whole of the lateral lobe: the second presented the most typical rolling movements and forced position for several weeks; in the first these were less marked, and in the third hardly to be observed at all. According to Risien Russell, who obtained similar results, this is due to the fact, that in the last case there is less increase or tension in the cerebellum than in the first. Apart from this influence of the tension, or perhaps partly dependent from it, there was found in these animals a different degree of degeneration of the tuberculum acusticum and the corpus trapezoides. The amount of degeneration in these bodies appeared directly proportional to the amount and vehemency of forced movements observed during life. The importance of the tuberculum acusticum, in regard to resulting forced movements, was already pointed out by Curschmann[1]. In these animals, as was the case in sharks and frogs, the rolling movements to the impaired side were many times associated with circus movements to the unimpaired side; in some cases when the rolling movements became less marked they were interrupted and usually replaced by circus movements to the unimpaired side, first with a smaller, later with a greater radius, the trunk being bent in the same sense, *i.e.* concave to that side.

The somewhat complex and at the same time important changes in the mobility of the eyeballs have not received sufficient attention in the work of preceding authors. (i) The deviation of the eyeballs in typical cases (after section of the right middle peduncle) is easiest to see in the rabbit, with its monocular vision. The right eye is deviated down and forward; the left eye is turned up and backward ("skew deviation" of R. Russell[2]). In the cat the right eye is turned down and to the right. The left eye is turned up and to the right. (ii) There is found constantly a rotation of the eyeballs around the visual axis. This is best studied in the cat with the slit-like pupils. If this animal, whose pupils normally slightly converge upward in such a way that their long axes meet about 4 inches above the head, is brought after the operation in front of some strong light, it is found that the eyeballs are rotated in such a way, that the lower portion of the

[1] *Deutsches Archiv d. klin. Med.*, XII. p. 356. 1874.

[2] *Phil. Trans. Royal Society*, CLXXXV. 1894.

vertical meridians deviates to the left, the upper portion to the right, a rotation therefore in the same sense as the rolling movements (Fig. 4, A, B). In the rabbit one finds with the same constancy the upper part

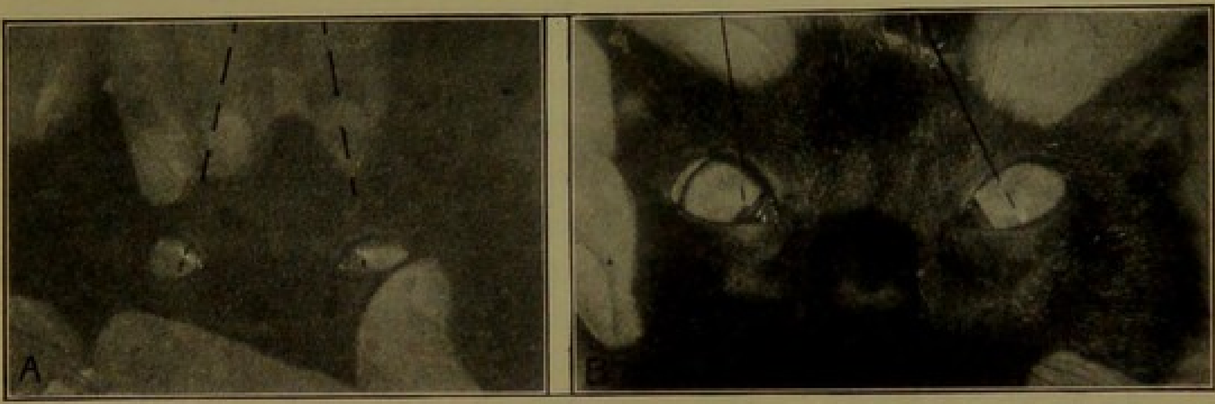

Fig. 4.

of the right pupil rotated backward, the upper part of the left pupil rotated forward. We notice therefore a most striking difference in the behaviour of the eyeballs of the cat on the one hand and the rabbit on the other. In the cat one finds both eyes deviated in the same horizontal direction and also rotated along the visual axis in the same direction; whereas in the rabbit not only the eyeballs deviate, the right one down, the left one up; but also the deviation in the horizontal plane, in contrast to the rotation around the visual axis, takes place in an opposite direction. It appears that the two entirely separate visual fields of the latter animal do account for a different way of coordination of the motor nerves of the eyeball. (iii) In the cat it is also easy to see that the rotatory nystagmus usually occurring in the earlier days after the operation is synchronous on the two sides, while the direction of the quick jerk of the nystagmus is directed *contrariwise* to the deviation above described; *i.e.* the right eye will jerk upward and to the left; the left eye downward and to the right. The rotatory jerk is equally directed contrariwise to the rotatory deviation. This form of nystagmus therefore is nothing else than a rhythmic jerking opposite to the direction of deviation and toward the normal position of the eyeball[1]. It will cease a few days after the operation and can then be

[1] It will be pointed out elsewhere that the nystagmus, elicited by operative lesion of some parts of the cerebral hemisphere, presents different features.

The form of nystagmus here alluded to is, as regards direction of quick movement, in striking contrast to that one of Gowers (*Transactions Ophthalmol. Society*, IV. p. 309), with a small diseased area on the R. side of the pons above the VIth nucleus, where the nystagmus was in the same direction as the deviation.

elicited again by rotating passively the head in a sense opposite to the deviation to which the head tends to rotate spontaneously. Another interesting fact, which may throw some light on this form of nystagmus, is that in deep ether narcosis the eyes are found to be deviated exactly in the same way, as it was found after the operation, but exactly to the opposite direction. In two cases the eyes had returned in three weeks quite in their natural position, and still this reversed deviation in the narcosis was very marked. To the frequent abnormal position of the eyeballs in ether narcosis Risien Russell[1] first called attention. He noticed in ether narcosis some time after ablation of the cortical area for conjugate deviation exactly the same deviation which was observed immediately after the operation.

As to the changes in the size of pupils, it may be recorded that after flocculus extirpation in cats and rabbits, the pupil on the side operated upon was markedly smaller than the other; the difference disappeared in three weeks. Then, during the narcosis a marked difference in the size of the pupils was noticed again, however in opposite sense; the pupil on the operated side was the larger one. In the cats, after ablation of the whole right lateral lobe and after section of the middle peduncle no such difference in the pupil was noticed.

As a rule the forced positions, in fact all the described phenomena, become more marked if the animal (especially the cat) is blindfolded with strips of plaster. In cases where a few days after the operation all symptoms of this kind have disappeared this proceeding will be found useful to bring back some of them.

In the case where the animal does not move spontaneously, information often can be got by simply rotating passively the head one way and the other; rotation to one side only opposes in some cases a special resistance. This or tendency to lie on one side only may under circumstances be taken as a sign of a tendency to a forced position, particularly if this is accompanied with eyeball symptoms.

Furthermore one may look for:

1. Deviation of both eyeballs to one side, of both eyes equally or one more than the other, either combined with the conjugated deviation of the head, clinically so masterly described by Prevost and Vulpian, or not;

2. Rotation of the eyeballs around their visual axis. I found this first in cats (see above), but it can be demonstrated also in the rabbit

[1] This *Journal*, XVIII. p. 1. 1894.

after having taken care to perform an iridectomy as a landmark (Fig. 5, A, B);

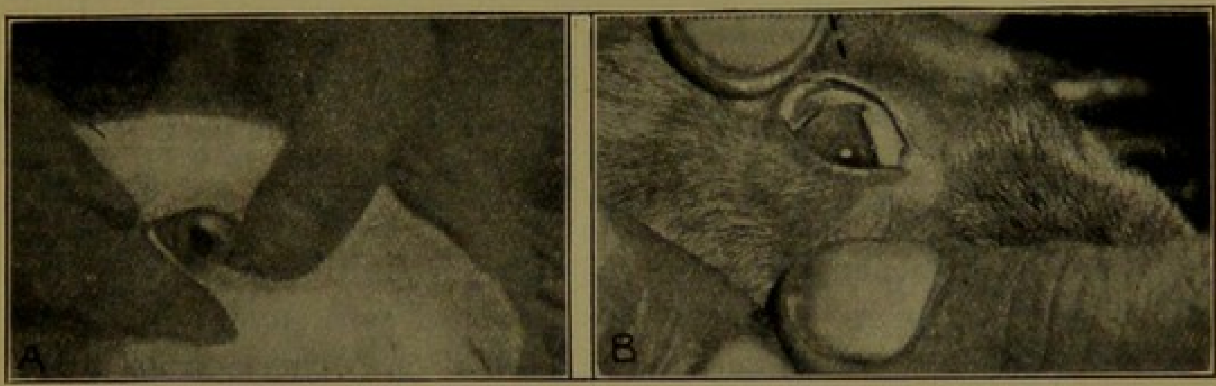

Fig. 5.

3. Certain forms of nystagmus:

(*a*) Continuous conjugated nystagmus (of both eyeballs), the rapid jerk being performed (*α*) in the same sense as the deviation of the eyeballs, or (*β*) in the opposite sense. The movements of the two eyeballs are not always of the same range and rapidity;

(*b*) Nystagmus which is elicited by looking to one side or trying to look to one side, or which is more marked while looking to one side than to the other;

(*c*) Nystagmus which is elicited by rotating passively the head to one side or to the other, or is different in character, range and rapidity, while the head is rotated to one side or to the other (see the following notes on a cat).

As I said before, the rolling takes place to the injured side with great constancy. With less constancy than in the lower vertebrates it is found that the circus movements resulting from said operations are directed towards the unimpaired side. Yet, quite comparable with what we found in sharks and frogs, the circus movements to the healthy side appeared in some cases to belong to the group of phenomena of which I tried to give a short sketch; in some other cases the two forms of locomotion were to the same side. In many cases when in the beginning very marked rolling movements were observed, they would after a few days subside and make place to circus movement to the other side.

As to the occurrence of rolling and circus movements after lesions of the cerebro-spinal axis, higher up than those which I have dealt with above, I must suspend detailed publication, as my observations are as yet not numerous enough. Yet I venture now already to make the following statements:

1. After lesions higher up than the optic thalamus (*i.e.* the cerebral hemispheres, striated bodies, etc.) rolling movements or allied forced positions are not met with except under very special conditions.

2. After various lesions of different parts of a cerebral hemisphere temporary circus movements with conjugate deviation of head and eyes to the same side are a very common occurrence. The direction of the circus movement is, in agreement with Magendie, Schiff, Reynal, Czermak, Vulpian, Prevost, Munk and Rossolimo, towards the side of the lesion. Sometimes these cerebral circus movements to the impaired side will be found accompanied with tendency to roll to the other side, or at least with a forced position in that sense. The head, therefore, will be found bent to the injured side and rotated towards the unimpaired side. Schiff found also, in agreement with Longet, that a lesion of the distal part of the optic thalamus and lesions below that level produced circus movement to the unimpaired side; of the proximal two-thirds of the optic thalamus to the impaired side[1].

The following are some of the notes of one of my experiments in a cat, to give some idea of the way in which the phenomena develop:

21.3.00. Cat ♀. Incision of skin along base of insertion of R. ear, under ether. Neck muscles removed. Cerebellum laid bare. After opening the dura, R. flocculus removed. As long as the narcosis lasts, nystagmiform jerks of R. eyeball, the rapid jerk being directed downward, are observed; the L. eye makes, synchronously with the R. eye, similar movements in opposite direction. Horsehair sutures. After the collodion dressing has hardened the animal is placed on the floor and makes rolling movements to the R.; after a while they are seen to be interrupted at times by circus movements to the L. The R. hind-leg appears to be somewhat atonic, tested by the swing experiment[2].

22.3. Staggers, shows some titubation. Placed on the floor the cat abducts the R. forelimb, to keep its balance. Head turned and bent to the R. Pupils R < L. Eyes rotated around their visual axis to the R. (Fig. 4 B). R. eye directed somewhat down, the L. eye upward. After a long rest, on stimulation of the cat's tail, it turns its head forthwith to the L., starts a circus movement to the L., but is, while doing so, interrupted by a rolling to the R. Nystagmoid jerks, conjugated on both sides. They are rotatory of character, the rapid jerk being directed in the sense of rotation to the L. Range and rapidity of the jerk are dependent from the position given to the head; if the head is rotated to the R. (*i.e.* the sense of the rolling movements) slow jerks of considerable range are observed, if the head is turned by the observer in the inverse sense the jerks are quick and of small range.

24. 4. 10 h. A. M. Head rotated to the R. Slow nystagmus (1 jerk in 2 and 3 seconds). Pupils as before. 11 h. 25′. After stimulation, circus movements to the L. If the head is kept in medium position and also if rotated to the R., hardly any nystagmus is observed;

[1] *Lehrbuch der Physiologie*, 1858, p. 354.

[2] *Neurologisches Centralblatt*, 1899, p. 1076.

it appears again if the head is rotated to the L. Dropped from 2 feet height back down, falls on R. side of body.

29. 3. No nystagmus in any position. Conjunctivitis on R. eye. Some loss of cerebro-spinal fluid from the wound. Optic discs normal. Usually the cat walks straight or to the R., whilst there is a tendency to fall on the R. side. As soon as blindfolded with plaster strips, the cat turns in a short circus (½ foot radius) to the L., while the forced position of rotation around the longitudinal axis to the R. increases. After removing the plaster the cat walks again to the R.

3. 4. Rotation of head and eyeballs less marked. Same experiment with blindfolding, with the same result.

9. 4. Idem. 12. 4. Pupils equal. Rotation of head and eyes persists. A marked resistance is still experienced while trying to rotate the head to the L. 10 h. 45′. Superficial ether narcosis. First the L., later also the R. eye, shows nystagmus, the quick jerk being directed to the R. Deep narcosis: rotation of eyeballs in opposite direction, as during life. L. eye somewhat turned up.

If by rapid bleeding death is caused in an animal which presents the complete syndrome of rolling movements to the right side (as well in cats as rabbits) a very marked asymmetry in the appearance of the rigor mortis is observed[1]. Careful notes were made about this phenomenon in a number of rabbits in Boston, March, 1898, in Prof. Bowditch's laboratory. While the animal is alive and rolling takes place to the right, the left hind-leg is, as a rule, in a state of greater tonicity than the right one; the head is, as said above, rotated to the right. After death the animal was suspended, at the ordinary temperature of the laboratory. Asymmetry in the state of tonicity was observed within 40′. Most constantly it was found that the left hind-leg remained quite limp, while the right hind-leg became quite stiff; this difference was especially marked in the flexors of the joints, whereas the extensors of the foot in two cases presented a change in the opposite direction. If there was found a marked difference in the condition of the fore-legs, the right fore-leg remained longer limp than the left one. It was also noted that it was easier to bend the head to the left than to the right. This asymmetry in the rigor mortis persisted for several hours.

In concluding this paper I may be permitted to explain how I have become accustomed to look upon the nature of the forced movements and allied phenomena. Having regard to the work of Y. Delage and others in arthropoda and my own experiments in octopods, I would

[1] The difference in rigor mortis of different muscle groups finds its expression in difference of the two sides of the body in the succession of the rigor in muscle groups and also in an asymmetrical degree of rigor; this can hardly cause any surprise, since the influence of severance of the peripheral and central nervous system of the rigor was studied by Nysten, and by Bleuler, Lehmann and Bierfreund.

suggest that all bilaterally symmetrical animals with independent locomotion are endowed with a system of nervous tracts and centres which enables the animal to perform the complicated action of locomotion, in which the coordination of vast groups of muscles is needed, in a well equilibrated way in three planes; asymmetrical lesions of this system cause the forced movements. The lesion may be localised either in the centripetal sphere of this system, otoliths and semicircular canals, or may affect one of the intracentral tracts. As to the centrifugal part of this system, which finds its leading centres in the mesencephalon and post- and methencephalon, there are signs that it has nothing directly to do with the pyramidal system, although it appears that nearly all voluntary muscles of the body are involved[1]. To the centripetal sphere of this system belong at least the otoliths, the semicircular organs, perhaps in some cases also the eyesight and the sense for touch. The importance of the semicircular canals and the vestibular nerve for all these phenomena is, I think, not open to doubt. It is well known (Flourens, Goltz, Ewald, Cyon) how lesions in any one of them results in marked abnormalities in locomotion and forced movements[2]. In Crustacea[3] as well as in the octopods it appears that the otolithic organ is the principal source of centripetal impulses for the nervous system for the equilibrium of locomotion.

In the Vertebrates with horizontal posture the most common movements are straightforward locomotion (*i.e.* in a line, which is the resultant of locomotion to both sides) and sideward locomotion. In regard to the free mobility of the body, rotation of head, eyes and trunk are most common. It appears to me that these complex movements are preformed in the central nervous system of all bilaterally symmetrical animals. Lesions of the particular tracts, which subserve these movements, *i.e.* locomotion in two most important planes, lead to forced movements, in the one case circus locomotion, in the other case rolling. Furthermore experiments give evidence that rolling to the diseased side is at least in the lower vertebrates in some way intimately related to circus movement to the other side. There is a difference,

[1] Brown Séquard (Rolling movements. *Course of Lectures.* Philadelphia, 1860) says that in most cases the principal cause is in the irritation of a certain set of nerve fibres, the division of which is not followed by paralysis, although they are able to act on muscles to produce contractions and even more powerful than those caused by nerve fibres, employed by the will in voluntary movements.

[2] Cf. B. Rawitz. *Engelmann's Archiv*, 1899, and v. Cyon, *Pflüger's Archiv*, LXXIX. p. 211, 1900, on turning Japanese mice.

[3] Delage. *Archives de Zoologie*, T. v. pp. 1—25. 1887.

however, between them in that rolling is never met with in lesions higher than the thalamencephalon or even the mesencephalon, whereas circus movement is also common after lesions of all parts of the hemispheres of warm-blooded animals. As the direction of circus movement after unilateral lesion of the distal parts of the cerebral axis is towards the unimpaired side and after lesion of the hemispheres towards the impaired side, we are led to believe that the particular tract in question crosses the median line in the mesencephalon, a conclusion to which also an experiment of Bechterew[1] must lead. As to the accurate place where this crossing takes place, it would be premature to discuss. In regard to the tracts whose functions are involved in the rolling movements and allied phenomena, it may be remarked, that the posterior longitudinal fascicle belongs to them, since Edinger, Held[2] and others showed the relation of this bundle to the 3rd nucleus of the same side, the 4th and 6th nucleus of the other side. This tract also is one of the first in acquiring its medullary sheath, in the lower as well as in the higher vertebrates, and on the other hand we noted above, that in the embryo of Raja, as well as in Vulpian's tadpoles[3], as early as locomotion at all is possible rolling movements can be elicited.

This system then, which we here refer to, whatever tracts may subserve it, has control of the above indicated forms of abnormal locomotion, and also of the compensatory movements of the eyes, in the case of active or passive turning of the head, and also causes reflexly, with the help of the vestibular nerve and its peripheral organ, involuntary movements resulting in maintaining the equilibrium of the body during any voluntary act. In regard to the fact, which I emphasized above for every class of animals in which I performed experiments, viz. that there exists a physiological connexion between rolling to the one and circus movement to the other side, I am led to believe that the mechanical conditions regarding the maintenance of the equilibrium of an oblong body necessitate this relation, the more so as this relation exists already in the earliest embryonic stages and appears to exist also in arthropods and cephalopods.

For reading through the paper and correcting the orthography the writer is indebted to Dr Swale Vincent.

[1] *St Petersburger Med. Wochenschrift*, 1882, p. 97.
[2] *Archiv für Anatomie (und Physiologie)*, 1893, p. 201.
[3] *Gazette Médicale de Paris*, 1862, p. 312.