fatigue. The measurements which were taken of the rates of velocity at different parts of the tracings afford somewhat varying results, and the number of cases is too few for any definite conclusions to be drawn from them. But it would appear that while the diminution is gradual and uniform in the case of small weights, in that of larger weights it occurs, as a rule, more rapidly, and that the rate of diminution does not remain the same throughout the tracing.

## VIII. "Experiments upon the Influence of Sensory Nerves upon Movement and Nutrition of the Limbs. Preliminary Communication." By F. W. Mott, M.D., F.R.C.P., and C. S. Sherrington, M.D., F.R.S. Received March 7, 1895.

In the 14th of the 'Leçons sur la Physiologie et la Pathologie du Système Nerveux,' Claude Bernard draws attention by experiments on the frog and on puppies to the degree of impairment in movement undergone by a limb that has been rendered insensitive by section of the sensory roots of its spinal nerves.

In a series of experiments carried out during the last eighteen months, we have examined the same thing in the monkey, using chiefly *Macacus rhesus*, and observing the animals for periods up to four months from the time of operation.* We propose to give here a brief account of the results obtained.

Our experiments deal separately with the lower limb and with the upper limb. The phenomena observed in the two limbs do not essentially differ, but are rather more marked and much more accessible to examination in the case of the upper limb.

### I. *On Movement.*

(1.) *Effect of Section of the whole Series of Sensory Roots belonging to the Limb.*—By the "whole series" is meant in the brachial region from the 4th cervical to the 4th thoracic inclusive; in the lumbar from the 2nd to the 10th post-thoracic inclusive.

From the time of performance of the section onwards, as long as the animal may be kept, the movements of the hand and foot are practically abolished; the movement of grasping, which is so frequent and useful to the monkey, both with the hand and foot, never occurs at all in our experience. On the other hand, the movements at the elbow and knee, and especially the movements at the shoulder and hip, are much less impaired. The fore limb hangs from the shoulder partially flexed at the elbow; the hind limb is flexed at hip

* In all our operations the animals have been deeply anæsthetised with chloroform and ether.

and knee. As the animal runs about it does not attempt to use the leg; the fore limb swings helplessly, with flexion at elbow and wrist and adduction at shoulder, in much the same position as if carried in a sling. The hind limb looks as if it were being held up so as to be kept off the ground while the animal runs on three legs; we are inclined to think that this appearance is deceptive, and that the position results from an equilibrium of the action of the muscles, in which purposive action on the part of the animal does not play a *rôle*. When the animal is allowed to climb a rope or the side of the cage, the fore limb swings more or less helplessly, and is not used for the climbing; similarly, the hind limb is kept more or less flexed at hip or knee, and is not used for the climbing. If the feeding-time be deferred, and an animal, in which the apæsthete* limb is an arm, be tested by offering it fruit after the sound arm has been secured behind the back, there is no attempt to use the apæsthete limb for reaching the food, but the neck is thrust forward in order for the mouth to seize it. If the fruit be placed in the hand of the apæsthete arm, the animal does not lift the hand, and appears quite unable to do so, even though encouraged. If, however, the hands of a tame normal monkey be secured behind its back, and, as it lies on the floor, fruit be placed near it, the fruit is usually taken at once with the foot; but if the leg is apæsthete the fruit cannot be taken, although in one monkey the attempt used to be made. The foot was rapidly thrust toward the fruit by extension of hip and knee, but the foot missed its object widely, *i.e.*, by several inches, and the digits were not moved, though the ankle appeared to be slightly plantar-flexed. The impairment of motility in the limb ensues immediately upon completion of the section; that is to say, directly the effects of the anæsthetic have passed off sufficiently to allow requisite examination of the animal's ability to move its limbs, the above-described inability is discoverable as fully developed as at any subsequent period. We have kept the animals alive for various periods up to and over three months, and there has been no obvious change in the condition, either in the direction of improvement or the reverse. In the case of the lower limb, after two or three months, the constant position of flexion of hip and knee, on two occasions, gradually induced a change in the muscles of the thigh, which prevented hip and knee being properly extended, even by passive stretching.

As to the nature of the disturbance of motility in the limbs, one feature, namely, its peculiar topographical distribution, is salient and constant. The defect in motility increases from the attached base to the free apex of the limb; so that, for instance, while com-

* Ἀπὸ, *αἰσθάνομαι*, "deprived of sensation," in distinction from anæsthete, "devoid of sensation." We are indebted to Dr. Verrall, of Trinity College, Cambridge, for the suggestion of this term.

paratively slight at the hip, it is successively greater at knee and ankle, and greatest (amounting as regards volition to absolute loss) in the digits.

In this respect it curiously closely simulates the impairment of motility ensuing upon ablation of the limb region of the cortex cerebri; but it is, in the monkey, somewhat *more severe* than the impairment following cortical ablation.

We find, however, that forcible and rapid movements, even of the fine joints at the end of the limb, can be induced in the animals by causing them to "struggle"; for instance, while recovering from ether inhalation, or while trying to free themselves on being held awkwardly, the whole limb at all its joints may exhibit movements; but even under these circumstances it is only once or twice that we have seen "grasping" movements of the digits, although sharp extension of the digits is not nearly so infrequent.

We are led from these and other considerations, which will be detailed in a fuller paper, to conclude that *associated movements in the limb* ("Mitbewegungen") *are comparatively little impaired* by loss of the sensation from the limb in which they occur; but that the independent and more delicately-adjusted movements which employ preponderantly the smaller and more individualised muscular masses of the hand and foot, and serve to move the digits, especially the hallux and the thumb—in fact, just *those movements which are represented most liberally in the limb area of the cortex, are extremely severely impaired, and, in some instances, are abolished.* We say 'abolished' advisedly, because we are persuaded from our observations that, in the case of certain movements, *e.g.*, grasping movements of the hand and foot, opposition of pollex and hallux, the animal is rendered absolutely powerless to perform them, even under the strongest possible inducements. This conclusion has been gradually forced upon us. Although we are aware of the danger of introducing terms relating to consciousness into descriptions based almost solely on motor reactions, we believe that we cannot more lucidly state the condition of the animals than by saying that the volitional power for grasping with the hand, &c., had been absolutely abolished by the local loss of all forms of sensibility experimentally produced. Further, that this volitional power was lost immediately from the time of operation, and that there was not the slightest evidence of any recovery of it during the longest periods to which our observations extended (about four months).

This being so, it is natural to inquire what influence, if any, is exerted by the section of the posterior spinal nerve-roots of the limbs upon the reactions obtainable from the limb area of the cortex? That no diminution, but rather a slight increase of the excitability of the cortex, is the immediate result has been shown by one of us

previously.* But the question remained, what will be the result when, for many weeks, the severance of the roots has led (as above shown) to disappearance from the limb of those very movements which the cortex, when experimentally excited, is especially able to produce? We have answered this, both by electrically exciting the cortex and by giving absinthe intravenously to produce epilepsy (Magnan). On exciting the cortex cerebri of the hemispheres in the appropriate regions for eliciting movements of the thumb, hallux, or digits, the responsive movements have been as easily elicited from the apæsthete limb as from the normal limb, and it has several times seemed to us rather more easily, that is to say, with a slightly less intensity of faradic current (the rate of interruption always remain-the same, $\frac{1}{60}''$).

As to the absinthe epilepsy, it always affected the apæsthete limb in a manner not distinguishably different from the normal limb. Convulsions sometimes started in the normal and desensitized limb simultaneously, sometimes a little earlier in one or the other; but no indubitable predominance or preference was shown by either limb. In a very few of our experiments (three) no movement was obtained in the apæsthete limb on excitation of the cortex; this was found to be explained subsequently by naked-eye degeneration of the pyramidal tract as revealed after hardening in Müller's fluid. This degeneration was due to injury accidentally inflicted upon the lateral column of the cord by the operation. The spinal tonus in the muscles of the apæsthete limb is undoubtedly much diminished.

These observations seem to us to point to the profound difference existing between the production of the finer movements of the limb in volition on the one hand, and by experimental stimulation of the cortex on the other. The fundamental importance of sensation for those finer movements of the limb, which are so especially well represented in the cortex of the ape, has by no authority been more forcibly emphasized than by Dr. Bastian. We think these experiments go even further than his arguments in pointing to the influence of sensation upon voluntary movement, inasmuch as they indicate that not only the cortex, but the whole sensory path from periphery to *cortex cerebri*, is in action during voluntary movement.

(2.) *Effect of Section of a single Sensory Root.*—In striking contradiction to the above-stated impairment of movement in the limb ensuing upon section of the whole series of its sensory nerve roots stands the effect of section of any one of the sensory nerve roots of the series singly and alone. In the latter case no impairment of movement at all results, or, at least, can with certainty be detected.

This is the case even when the largest and most important sensory

* C. S. Sherrington, 'Phil. Trans.,' vol. 184, B, pp. 690, 691.

root of the series is chosen for section; namely, in the upper limb the 8th cervical, and in the lower limb the 6th post-thoracic. (These are the nerves that supply the skin over the whole of the hand and foot respectively. It is to be remembered, however, that hand and foot respectively are each of them supplied with sensation by at least three sensory roots, the middle root covering the whole surface in each case.)

We attribute the fact that section of these large roots with their wide distribution over hand and foot produces so little appreciable effect, to the fact that the distribution of all the spinal nerves in the skin is an overlapping one. The extent of overlapping is great enough to prevent the section of any one nerve, even of the largest, producing actual anæsthesia of the skin in any part.

We further find that even if a field of absolute anæsthesia be actually produced by section, for instance, of the 7th, 8th, and 9th post-thoracic roots, or, in some cases, by section of the 7th and 8th cervical and 1st and 2nd thoracic roots, the impairment of movement resulting in the limb is comparatively slight. This is the more remarkable when the region deprived of sensibility includes some of the most highly sensitive parts in the limb, namely, those of the palm.

In such a case the retention of sensibility, although in an impaired degree, by the radial side of the palm, including pollex, is the cause, in our opinion, of the remarkable quantity and quality of movements still executed by the limb in spite of that impairment. In the case of section of the 7th, 8th, and 9th post-thoracic sensory roots, it was almost impossible, even on the closest examination, to detect any defect of movement whatever; the animal used both its feet apparently equally well in climbing or running, there was no clumsiness in picking up small objects (as a kernel) with the foot, and no hesitation in so doing. The chief detectable muscular difference between the limbs was that the knee-jerk was more brisk upon the operated side, and the calf and ham and back of the thigh were very deficient in sensation.

In the case of section of the sensory roots of the 7th and 8th cervical and 1st and 2nd thoracic, besides the ulnar border of the arm, the hand, with the exception of the thumb and radial side of index, is also quite insensitive; and the sensitiveness of the skin of the thumb and index, where present, is below normal in degree. Nevertheless, although impairment of movement (especially clumsiness) is obvious, yet the condition is strikingly different to that obtaining after the whole series of roots has been cut through. Food is easily taken up from the hand and picked up from the floor with the thumb and index of the partially apæsthete limb, and the limb is freely used in progression and in climbing. The grasp of the partially

apæsthete hand is easier, however, to detach from the cage than that of the normal hand.

We find, again, that a degree of impairment very nearly as great, indeed not obviously different from that produced by section of the sensory roots of the whole series of the nerves of the limb, is produced by section of just those sensory roots which supply the apex of the limb, *i.e.*, the hand and foot. If the whole hand or foot be completely apæsthete by the sections, then the peculiar degree of inability to move the limb, described at the outset of this communication, is obtained in (as far as we can see) its full extent. This result has its converse in the following, which we have also noted:—

(3.) *Effect of Section of the whole Series of Sensory Roots belonging to a Limb, with the exception of a Root that supplies the Hand or Foot.*—If the sensory roots of the whole series of the spinal nerves belonging to a limb be severed, with the single exception of, in the upper limb, the 8th cervical (distributed to the whole extent of the hand), and in the lower limb the 6th post-thoracic (distributed to the whole extent of the foot), a certain degree of impairment of movement of the limb results, which appears rather as weakness than clumsiness, but the degree of impairment is altogether quite slight. The limb is used freely for progression, for climbing, for picking up food, and bringing it to the mouth. The grasp of the partially apæsthete hand is easier to detach from the cage than that of the hand of the normal side.

The question naturally arises whether in the interruption of the paths of afferent impulses these can be so dissociated as to decide what share the muscular sense takes in the results observed? The afferent nerve fibres from muscles *per se* run, in every case in which they have been examined, in the corresponding spinal roots to the motor. It is possible, therefore, in the hand and foot to sever the sensory roots supplying the muscles, while only partially interfering with those supplying other structures—the skin, sheaths of tendons, joints, &c. The converse is also true. On leaving intact the afferent fibres from muscle for the greater part, but interrupting all other afferent channels, we find that the defect of movement produced is nevertheless extreme, as, for instance, when the lowest four cervical and the first thoracic roots are severed. In the same way, when the 5th, 6th, and 7th post-thoracic roots are divided, the sole of the foot is apæsthete, and the defect in movement is extreme, although the afferent fibres from the plantar muscles remain to a large extent intact.

Conversely, when the 7th, 8th, and 9th post-thoracic roots are severed, the afferent fibres from the plantar muscles are completely interrupted, but the sole of the foot remains sensitive all over, owing to the 6th and 5th roots. In this case (and we have two instances of the kind), the defect of movement, if it exists at all, is not appreciable.

It must be remembered that other deeper structures are innervated by the same nerves as the skin, and these we do not wish to dissociate from the sensory channels still uninjured after interruption of all afferent tracts from the muscle itself.

## II. *On Nutrition.*

In the experiments upon the lower limb we were at first led to suspect that section of the sensory roots caused trophic changes in the skin of the foot. After a time, varying from three weeks to three months, an ulcer appeared over the outer malleolus; the subsequent experiments on the upper limb, which never led to such a change, show, in our opinion, that the apparent trophic change in the lower limb may more justly be attributed to the liability to pressure and microbic infection. No change in the hand was ever noticed which in the least indicated trophic disturbance. Wounds accidentally inflicted by the animal itself or its companions on the apæsthete part healed readily when dressed.

As to the condition of the muscles in the apæsthete limb, which were themselves removed from all afferent connection with the central nervous system, the following points were noticed :—

There was a certain degree of wasting, but no appreciable alteration of colour ; and the muscles responded readily to the excitation of their motor nerves. In some instances it was found that on excitation of their motor nerves, after somatic death, muscular contractions were evoked for a longer period than on the normal side. The time of onset of *rigor mortis* was delayed in the apæsthete muscles, as one of us has already noted in the cat.*

## III. *Preliminary Note on the Degenerations observed.*

It is of interest to remark that the bulk, if not all, the fibres of Goll's column are derived from those sensory roots which contribute to the innervation of the lower limb. Certain of the sensory fibres innervating the limb enter, therefore, into the formation of a path leading directly to the cortex by the *posterior column nuclei*, the *fillet*, and the *optic thalamus*.

On the other hand, section of a short series of five dorsal and upper lumbar roots produced no appreciable degeneration in Goll's column. This appears to us a most suggestive fact, because the fibres from the limb thus entering Goll's column contribute to a path which leads *viâ* Goll's nucleus and the fillet to the opposite optic thalamus and cortex of the central convolutions. But the fibres from the roots above those entering the limb not contributing to Goll's column, their

* C. S. Sherrington, 'Roy. Soc. Proc.,' vol. 53, p. 408.

upward path must be *viâ* grey matter, and probably subsequently by one of the cerebellar tracts to the cerebellum.

In the cases of section of the brachial and upper thoracic posterior roots no degenerated fibres go into Goll's column, nor into Goll's nucleus, but there is very extensive degeneration of Burdach's nucleus. The upward path from the arm resembles therefore that of the leg in respect to its upward projection toward the cortex.

One of the chief results to which, in conclusion, we wish to draw attention is the following:—That afferent impulses, both from the skin and from the muscles, especially the former, as related to the palm and sole, are necessary for the carrying out of "highest level" movements.

It may be argued against this assertion that in animals it is impossible to obtain definite information as to whether the animal *can* not or *will* not perform the movements the absence of which has been described.

From observations on tame animals we are, however, ourselves firmly convinced that there exists actual inability to perform the movements in question. The reasons for this belief will be detailed in our fuller paper.

## IX. "On the Development of the Branches of the Fifth Cranial Nerve in Man." By A. Francis Dixon, B.A., M.B., Chief Demonstrator of Anatomy, Trinity College, Dublin. Communicated by Professor D. J. Cunningham, F.R.S. Received February 22, 1895.

(Abstract.)

The investigation, the general results of which are summarised below, was suggested to the author by Professor His, and part of the work was carried on in his laboratory in Leipzig in the summer of 1893. Models were constructed of the cranial nerves in embryos of different ages, and the branches present noted and measured. These models were made up of glass plates, covered with varnish, on which were drawn the outlines of the sections and the positions of the nerves, &c. Detailed descriptions of the fifth nerve branches are given for five different stages of the human embryo, beginning with an embryo of four weeks, at which time merely the three main divisions of the nerve are represented, and ending with one of the eighth week. The observations on the human embryo have been checked by further observations on rat embryos, and an almost complete correspondence between the two has been made out.