NOTES ON THE ARRANGEMENT OF SOME MOTOR FIBRES IN THE LUMBO-SACRAL PLEXUS. By C. S. SHERRINGTON, M.A., M.B.

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NOTES ON THE ARRANGEMENT OF SOME MOTOR FIBRES IN THE LUMBO-SACRAL PLEXUS. By

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SECTION I.

AT the commencement of some observations on the reflex mechanisms of the spinal cord in the Monkey, I was met by difficulties which made it desirable to attempt for that animal a somewhat particular examination of the distribution of the efferent and afferent spinal nerve-roots belonging to the lower half of the body. Various interruptions incidental to the work have delayed its progress sufficiently to make one desirous to record at this time some of the results obtained. The present communication has reference chiefly to the distribution of the efferent fibres of the roots.

For the study of the functions of the spinal cord, it is of importance to know accurately the positions of the central and peripheral structures between which the fibres of the spinal nerves constitute links. An examination of the distribution of the efferent roots promises the more interest since the researches of Ferrier and Yeo[1] have led those observers to conclude that the complex of efferent fibres gathered together in each motor root is the outcome and the representative of some one "highly coordinate functional synergy" in the musculature.

[1] *Proc. Roy. Soc.* March, 1881.

Analysis of the motor root will in that case mean analysis of a functional motor combination of high physiological significance.

The fine interchange of filaments between nerve trunk and nerve trunk, and the *détours* and loopings which nerve filaments exhibit in the course of their distribution through a plexus, are too intricate for unravelling by dissection and the methods of descriptive anatomy; much assistance can however be rendered by physiological methods. It is true that physiological experiment in this field can only by analogy be applied to the particular case of man, and that it is precisely the case of man that imbues the problem with greatest practical interest. In certain regions of the human body the skilful care of the dissector has achieved much; but discrimination between afferent fibres and efferent fibres is unfortunately at present beyond the power of anatomy. In the case of man, the facts won by pure anatomy have been illuminated at various points by evidence afforded in disease, and in the accidents of injury (cf. Thorburn's valuable *Surgery of the Spinal Cord*). The interpretation of this pathological evidence is however generally difficult, and the accumulation of sure knowledge from such a source, as regards many regions of the body, extremely slow of progress.

Previous Observations.

It is nearly sixty years since a remarkable letter was written by Panizza to Maurizio Buffalini in Pavia (*Annali Universali di Medicina*, 1835). In it together with various experiments in examination and extension of Majendie's and Bell's observations on the sensory and motor roots of the cerebro-spinal nerves, there are related what appear to be the earliest physiological experiments on the arrangement of the nerve fibres of the spinal roots in the nerve plexus of a limb. As to the significance to be attached to nerve plexuses, various hypotheses had been advanced by Reil[1], Scarpa[2], A. Monro[3], Soemmering[4], and others, but it is unnecessary to dwell upon them here as they are conjectures unsupported by evidence.

Panizza's letter states as a remarkable fact regarding the arrangement of the motor fibres of the lumbo-sacral plexus, that when one anterior root only is cut, "la facoltà moscolare dell' arto continua a mani-

1 *De Nervorum Structura*, p. 14.

2 *De Gangliis et Plexibus.*

3 *Observations on the Structure and Functions of the Nervous System*, p. 34.

4 *Anatom. Pars quinta.*

festarsi, anche subito dopo l'operazione in tutta la sua vigoria." When even as much as two-thirds of the nervous mass which is distributed to the muscles of one or several joints is cut away, the movements of the limb, although assuredly weakened for the moment, in a short time return with all their original vigour, "sicchè l'animale corre e salta come se nulla avesse sofferto. Basta in fine rimangli un solo filamento, perchè gli movimenti gradatamente ricuperino la usata forza; troncato il quale, cessa nella parte immediatamente ogni moto." This peculiarity of the motor nerves must mean, Panizza suggests, that the innervation determining the movements of a limb is based on a number of nerve roots which have community of function, so that the quality of the conduction chain between the motor mechanisms of the spinal cord and muscles of the limb remains the same whether all the roots or only one be present, but the size of the path is less in the latter case, and the rate of conduction along it is slower. "D'onde, se male non mi appongo, apparisce l' uso dei plessi nervosi, per l' immischiamento che fanno dei filamenti di diverse radici aventi una funzione medesima, quando per una lesione qualunque venga interrotta la continuità degli altri filamenti."

He thus supposes each original motor "filament" entering into a plexus is capable of maintaining in its integrity the motor function of the whole plexus; and that the purpose subserved by the plexus is the assurance of alternative accessory paths in case of injury. According to him then the limb plexus has a physiological rather than an anatomical significance.

On the other hand, John Müller at the same epoch wrote, "through the plexus definite aggregations of nerve fibres for definite natural groups of motile and sensitive parts are combined, and the further distribution of any one nerve to a group rendered easier. The latter combination it is possible to consider simply as anatomically convenient and the outcome of the position of the parts." Thus Müller inclines to an anatomical significance for the plexus.

In the first edition of his *Handbuch der Physiologie des Menschen*[1], Müller (nach eigener Untersuchung) laid down as one of the laws of conduction of the nervous principle along motor nerves that "a spinal nerve that enters a plexus and contributes with the other spinal nerves to a large nerve trunk imparts its motor power not to the whole nerve trunk but only to those fibres with which it is continuous within

[1] Vol. ii. (1834) p. 685 Abschnitt 3.

the nerve trunk and its branches." He referred to experiments on the lowest four nerve roots of the frog. He wrote "One excites the nerves separately either mechanically with a needle or with galvanism by letting both poles act on the nerve, and the current go through the thickness of the nerve, while each nerve that contributes to the plexus is isolated from the rest on a glass plate." Of the three nerves which form the plexus of the hind limb, the first when excited causes twitches on the inner side of the thigh, the second "twitches of the muscles of the thigh and leg, but not of the foot, the third movements of the thigh, leg, and foot."

Van Deen[1] arrived at conclusions similar to Müller, but experimented by a different method. He separately cut through each nerve entering into the sacral plexus of the frog, and found that in spite of the communications of the nerves, different muscles were paralysed. After section across the N. inguinalis the frog performed all movements of the limb except flexion of the hip; after section through the 2nd nerve of the plexus the movements of the thigh and leg were lost, but those of the foot remained. After section of the 3rd nerve of the plexus the foot, and in part the leg below the knee, was paralysed. If the sciatic nerve were split down along its length, there ensued a paralysis as complete as if the whole sciatic had been cut across.

In 1834 the medical Faculty of Berlin offered a prize for a work on the following theme:

"Indagentur structura et virtutes plexuum nervorum; anatomica et microscopica observatione exquiratur, utrum fibrillae quae vocantur primitivae nervorum plexum brachialem, lumbalem sacralemve intrantes, in ipso plexu confluant, an sine vera earum anastomosi solummodo decussentur misceantur novo ut ordine prodeant; praeterea experimentis in animalibus frigidi calidive sanguinis instituendis evincatur, utrum irritatio in nervum, qui plexum intrat, agens per consensum in toto plexu et per nervos inde oriundos ad omnes musculos propagetur, an irritatio nervi intrantis per aliquas solum plexus partes in continuatas ejusdem nervi fibrillas singulosque musculos agat: unde natura plexuum nervosorum eorumque differentia ab anastomosibus vasorum dilucidetur."

There is little doubt that it was at the instigation of John Müller himself[2] that the theme thus announced was set. To the essay of H.

[1] Van Deen. *De differentia et nexu inter nervos vitæ animalis et organismi.* Leyden, 1834.

[2] Cf. Kronenberg, p. 2. "Primas rei propositae lineas illustrissimus Prof. Mueller adumbravit."

Kronenberg the prize was awarded in 1836. His work was the result of lengthy investigation carried on both by dissection and excitation. Dissections were made upon the brachial plexus of man and the rabbit: excitations on the brachial nerves of the rabbit and the lumbo-sacral of the frog. Nine dissections of the brachial plexus of man simply confirmed three by Scarpa, and four by Haller, in the *De Gangliis et Plexibus*, Lib. I., showing that the contribution of the various spinal roots to the chief nerve trunks of the plexus is not quite constant, and that the more common arrangement is as follows:

Suprascap. 5, 6.
Musc. cutan. 5, 6, 7.
Median 5678 or 56781.
Ulnar 56781 or 781 or 81.
Axillary as often 56781 as 567.
Radial as often 56781 as 678.
Int. cut. 81.

On the brachial plexus of the rabbit his anatomical work yielded no result that need be remarked upon here except the comment that he did not, any more than his predecessors, detect the contribution from the 2nd thoracic to the plexus which is so commonly present. As to the question whether primitive nerve fibrils, which Fontana[1] had shown not to remain separate from one another in their course along the nerve trunks, become united together in plexuses or become only juxtaposed by decussation, his search with the microscope led him to confirm the previous opinion of Müller and Van Deen that they are juxtaposed not united, "Verbinden sich die Primitivfasern unter sich niemals, so steht das Hirnende einer Primitivfaser immer auch nur mit einem einzigen peripherischen Ende in Zusammenhang und dem peripherischen Ende entspricht nur eine einzige Stelle im Gehirn oder Rückenmark."

Kronenberg's experiments on the rabbit consisted in laying bare individual cervical nerves and exciting them either by mechanical or galvanic stimuli. He noticed by inspection which muscles twitched: on stimulating 5th cervical; lat. dorsi, triceps, deltoid, teres.

6th cervical; lat. dors., triceps, biceps, pronator, and the flexors of the hand.

7th cervical; lat. dors., pect., teres, deltoid, triceps, biceps, brach. int., extensors of forearm.

[1] *Sopra il veneno della vipera.* Lucca, 1777.

8th cervical; pect., lat. dors., teretes, triceps, flexores man. et digit. pronat. rot. biceps, extensores man. et digit.

1st thoracic; same as 8th cervical.

Two of his conclusions are the following. 1. The excitation of a single nerve root before its entrance into the plexus produces contractions of almost all the muscles of the limb. In this way the spinal cord is able from any point whence a cervical nerve springs to bring about the most different movements. Hence only a little part of the central organ is put under strain or tired, in order to bring about coordinated work and movement. 2. The plexuses support the power and endurance of the central nervous system and prevent their too quickly tiring, because when coordinate movements are to be set going another part of the central organ which represents the same movements can function when the first part is exhausted.

By Kronenberg's work a fundamental question found a definite answer. Do the primitive nerve-fibrils actually fuse in a plexus? Müller in his text-book in 1834, believed the answer to be "no." Panizza agreeing with Fontana had believed "yes." Van Deen on the other hand supported Müller, and Kronenberg demonstrated the correctness of Van Deen's and Müller's opinion.

The next step taken was by Eckhardt. He examined the sciatic plexus of the frog. The following are the more important of his results and conclusions[1].

Excitation of the whole 8th root of Rana causes flexion of ankle, with extension and bringing together of toes. Stimulation of whole 9th gives flexion and opening apart of toes.

A great number of muscles obtain nerve-fibres, each of them from several nerves; there is a good deal of individual variation. Most of the thigh muscles almost always, some of the leg muscles sometimes, from three spinal nerve roots. "Ist ein Nerv unverhältnissmässig dick, so werden die überzähligen Fasern nicht alle oder vielleicht gar nicht dazu verwendet dieselben Muskeln mit mehr Fasern sondern mehr Muskel als gewöhnlich zu versehen."

"Es findet nicht allgemein eine Vertheilung der Fasern verschiedener Nerven in der Weise statt, dass die des einen zu einer bestimmten Muskelgruppe von gleichartiger Function, während die eines andern zu einer andern gingen; ja es liegen sogar in einer oder derselben

[1] *Zeit. f. rat. Med.*, Vol. VII. p. 306, 1849.

Nervenbahn Fasern die zu Muskeln von entgegengesetzter Function bezüglich eines u. desselben Knochens gehen. Denn in der Bahn des 7ten liegen Beuge- und Strecknerven zugleich der Zehen."

Eckhardt made his research in C. Ludwig's laboratory. Three years later at Ludwig's suggestion the Medical faculty at Zurich offered a prize for a thesis on a similar theme. *In which muscles and in which parts of the skin do the nerve roots that enter into the formation of the brachial plexus terminate?* The prize was awarded to J. Peyer in the following year. His research was carried out upon the rabbit, under Ludwig's direction. Peyer[1] used for excitation weak induction shocks and electrodes sheathed to their tips.

Peyer's conclusions were:

Most muscles receive their nerve fibres from more than one, occasionally indeed from three, nerve roots. Sometimes the contraction of a muscle on excitation of different roots innervating it is obviously of different degree.

One and the same root does not always supply in different individuals exactly the same muscles, but the variation is slight and does not seriously disturb the general picture of the contracting group.

Muscles which are near together receive their motor fibres from nerve roots which are near together,—an exception to this being the M. extensor carpi internus.

Nerve roots leaving the cord further back supply progressively muscles lying nearer the hand.

One and the same nerve root is not devoted exclusively to the excitation of a muscle complex such as denoted by the term Extensors, Flexors, &c. The same nerve root supplies with sensory fibres as a rule those parts of the skin beneath which lie the muscles it innervates.

Eight years later Krause[2] repeated Peyer's work, using the same limb and the same species. He modified Peyer's conclusions in several minor points. The combined results of the two writers may be tabulated thus:—

[1] J. Peyer. "Ueber die peripherischen Endigungen der motorischen u. sensiblen Fasern der in den Plex. brach. des Kaninchens eintretenden Nervenwurzeln." Zurich, 1853. *Arch. f. rat. Med.* II. iv. 67, 77.

[2] *Beiträge zur Anatomie der oberen Extremität.* 1861.

Name of muscle.	C 5	C 6	C 7	C 8	D 1
Arm					
M. latissimus dorsi			+	+	
M. teres major			+		
M. subscapularis		+	+		
M. pectoralis major			+		
M. pectoralis minor		+	+		
M. deltoides	+	+			
M. supraspinatus	+	+	+		
M. infraspinatus		+	+		
M. teres minor		+	+		
M. abductor brachii superior		+	+		
M. abductor brachii longus		+	+		
M. coracobrachialis		+			
M. extensor parvus antibrachii				+	+
M. anconaeus			+	+	+
Forearm					
M. pronator			+		+
M. flexor carpi internus			+	+	+
M. flexor digit. prof.				+	+
M. flexor digit. subl.				+	+
M. palmaris				+	+
M. flexor carpi externus				+	+
M. abductor carpi				+	+
M. extensor carpi externus				+	+
M. extensor digit. communis				+	+
M. extensor pollicis				+	
M. extensor carpi radialis		+	+		
M. adductor carpi				+	+
M. flexor digiti minimi					+
Hand					
Mm. lumbricales					+
Mm. interossei					+

Further important conclusions arrived at by Krause were the following:

i. The so-called nerve trunks are in truth nerve plexuses, the meshes of which have very acute angles, both toward the cord and toward the periphery[1].

ii. The larger muscles are supplied by nerve fibres from several nerve

[1] Of this his book contains an excellent plate in illustration.

roots. They stand therefore in connection with various segments of the spinal cord.

iii. The parts of the upper extremity which are nearer the hand receive their nerve fibres from roots which are nearer the lower end of the cord. This is true of the sensory as well as of the motor fibres. The absolutely longest nerve fibres come from the 8th cervical nerve.

iv. The muscles receive the nerve fibres from the spinal nerve roots which supply the skin over them and their tendons, the muscle fibres belonging to the several tendons receive separate nerve trunks, which may take their origin from different nerve roots.

v. Regarding abnormal nerves, it appears that abnormalities only occur in the course of the nerves from the centre to the periphery—the final distribution at each end remains invariable.

The intrinsic muscles of the foot are, according to Peyer and Krause, in the rabbit innervated from one nerve root only, namely the first thoracic. Later, in his *Anatomie des Kaninchens* (1868) Krause mentions that a branch from the second thoracic nerve goes to the plexus, but concludes that it is too small to modify the results already published by him.

After the appearance of Krause's monograph on the roots of the brachial plexus, sixteen years elapsed without further contributions of the kind. Then, in March, 1881, Ferrier and Yeo[1] published an account of excitation experiments on the roots of the limb plexuses in monkeys. Their results are too well known to require detailed description here. Their observations relate chiefly to the movement produced by the excitation of the root, and deal less with the particularisation of the individual muscles involved. Their observations may be epitomised for the purposes of this paper as follows, the correction published by themselves two years later for the numeration of the roots of the brachial plexus being incorporated.

5th cervical. Elevation and retraction of the arm, flexion and supination of the fore-arm; by the rhomboids, spinati, biceps, brachialis and supinators.

6th cervical. Similar to the last, but without retraction of the arm, and with extension of the wrist and first phalanges; by the deltoid serratus, flexors of elbow, extensors of wrist, and long extensors of fingers.

7th cervical. Adduction and retraction of the upper arm, extension

[1] *Proc. Roy. Soc.*

and pronation of the fore-arm, flexion of the wrist; by contraction of the pectoralis, latissimus dorsi, triceps, flexors of wrist, pronators.

8th cervical. Adduction and rotation inwards at the shoulder-joint, flexion of the wrist, and of the fingers at the second phalanx by the teres major, latissimus dorsi, subscapularis, triceps, and long flexors of the fingers.

1st dorsal. Flexion of fingers and thumb so as to close the fist; flexion of wrist towards the ulnar side, pronation of fore-arm, extension of elbow; by the intrinsic muscles of the hand, the long flexors of the fingers and thumb, the flexors of the wrist, and the triceps.

2nd dorsal. Adduction of the thumb, flexion of the fingers at metacarpophalangeal joints; distal phalanges slightly extended, fingers spread.

On the lumbo-sacral roots experiments were performed by Ferrier and Yeo, six in number. Two of the experiments were, they state, incomplete. What species of monkey was used is not mentioned. They did not include the 2nd sacral root in their experiments: this root however undoubtedly goes into the limb plexus.

1st sacral. Adduction and flexion of hallux (basal phalanx), flexion of the proximal phalanges of the toes, with slight separation and extension of the distal phalanges. The tail moves to the same side.

7th lumbar. Flexion of the leg (hamstrings), plantar flexion of the foot (sacral muscles), adduction of the hallux and flexion of the proximal phalanges (as in 1st sacral) with the addition of flexion of the hallux at the distal phalanx (long flexor). Thigh slightly rotated outward. The tibial and peroneal muscles and long flexors of the fingers do not act.

6th lumbar. Rotation outward of the thigh (which assumes a position midway between extension and flexion), flexion of the leg with inward rotation, plantar flexion of the foot with flexion of the hallux and toes at their distal phalanges. The outer edge of the foot is somewhat raised. Action of muscles in the gluteal region, the hamstrings, sacral muscles, long flexors, tibialis anticus and posticus, the peroneal muscles and the extensors of the toes.

5th lumbar. Extension of the thigh, extension of the leg, and pointing of the great toe. Muscles in action are gluteal, adductors, extensor cruris, and peroneus longus.

4th lumbar. Flexion of the thigh on the pelvis, extension of the leg. Muscles in action are the sartorius, adductors, extensor cruris.

3rd lumbar. No action on the leg.

2nd lumbar and 1st lumbar. Contraction of some muscles in the flank and hypogastric region.

In July of the same year Paul Bert and Marcacci[1] published the results of excitation-experiments in the cat and dog on the motor roots of the lumbar region. These results were as follows:

1st lumbar. Sartorius, rectus, psoas. Flexion of hip.

2nd lumbar. Anterior part of Vastus externus, Vastus internus, Tensor fasciae latae. Extension of knee.

3rd lumbar. Part of Vastus externus, anterior portion of biceps, (not posterior portion; the anterior part extends the limb, the posterior part flexes it).

4th lumbar. Posterior part of biceps, semitendinosus, semi-membranosus. Flexion of knee.

5th lumbar. To the tail.

They concluded from their experiments (i) that each root produces a coordinate movement and consists of fibres functionally associated, (ii) that only when a muscle is functionally divisible its nerve supply is multi-radical; e.g. biceps cruris.

In 1883 Forgue and Lannegrace published researches on the distribution of the motor roots to the limb muscles. Their first communication seems to have been in the *Gazette Hebdomadaire des Sciences Médicales de Montpellier*[2]. To a copy of this I have not been able to refer. The *Comptes Rendus* for the following year[3] however contains three reports of their experiments by themselves.

As to the upper limb they make an epitome based on experiments in the dog and in the monkey from which I extract the following:—

1st thoracic. "(1) à l'innervation du fléchisseur sublime, du fléchisseur propre du pouce, de la partie extrême du fléchisseur profond et des muscles de l'éminence thénar; (2) du cubital antérieur, de la partie interne du fléchisseur profond, des muscles de l'éminence hypothénar et des interosseux, (3) des muscles de la région postérieure de l'avant-bras." They do not recognise that the 2nd thoracic root innervates the hand and forearm in the monkey.

Their account of the distribution to the lower limb is more brief. It is prefaced by the remark that the highest lumbar root of man is tripled in the dog and monkey. The results obtained from those animals are translated into the nerve-roots of man on that supposition. As I am not disposed to agree with their view that the first lumbar

[1] *Soc. de Biol.* July 29, 1881. Also *Lo Sperimentale.* Oct. 1881.
[2] No. 5. 1883.
[3] p. 685 and p. 1068. 1884.

nerve of man is represented by three in monkey, it has seemed best to give their results in their own words but in the actual numbering of the nerve roots of the monkey.

The first, second and third do not contribute to the limb in dog or monkey. The 4th: (1) à l'innervation du psoas-iliaque (fortement) du pectiné, du couturier du droit antérieur, du vaste interne, (2) du droit interne et du premier adducteur. The 5th: à l'innervation (1) du psoas-iliaque, du couturier du droit antérieur, du vaste interne et du vaste externe, (2) de toute la masse des adducteurs et du droit interne. The 6th: à l'innervation (1) du psoas et du vaste externe; (2) du grand adduct., (3) des muscles fessiers, du biceps, du demi-membraneux, du demi-tendineux, du grand adducteur, du jambier antérieur, des extenseurs des orteils et des peroniers; faiblement à l'innervation du triceps sural, du long fléchisseur commun des doigts et du long fléchisseur propre du gros orteil. The 7th: à l'innervation (1) des muscles fessiers, (2) des muscles fléchisseurs du jarret, (3) du triceps sural, du jambier postérieur et des fléchisseurs des orteils. The 8th: à l'innervation de tous les muscles de la région postérieure, de la jambe et de la région plantaire. The 9th: à la même fonction que la précédente.

In the *Comptes Rendus*, the authors declare the following conclusions, based on their experimental observations on the two limbs. The majority of muscles are innervated by several roots.

Excitation of a root determines in the muscles which it supplies a total, not a partial contraction. The tributary fibres of the root are disseminated through the muscle supplied by it and not "cantonnée" in a special zone of it.

Each root has a muscular distribution almost absolutely constant in the animals of its own species. The functions of analogous roots differ very little in different mammalian species.

Each root supplies muscles of very various, often of antagonistic action. Excitation of a root gives a combined movement but this movement is artificial not functional.

The roots that pass furthest into the member occupy the lowest position in the cord. The innervation of the two planes of flexors and extensors is not always symmetrical. The superficial layers are supplied before the deep. As the stimulation of the brachial roots approaches the dorsal region the contractions pass from the radial to the ulnar border.

It is curious that these authors do not remark that the roots of the cat and dog and monkey do not in the lower limb correspond: they apparently consider them to be equivalent number for number. It is not stated in their report what species of monkey they employed.

In 1887 appeared a paper by Herringham[1] which has an intimate bearing on the present theme, although it deals only with the upper limb plexus and is based on the method of naked-eye dissection. The paper treats of the anatomy of the human brachial plexus examined in some fifty individuals. The results naturally labour under disadvantage from inability to distinguish clearly between afferent and efferent nerve fibres; but the facts and conclusions are nevertheless very valuable. Herringham proceeded to the formulation of certain "Laws." Of these the first runs, "any given fibre may alter its position relative to the vertebral column but will maintain its position relative to other fibres." The second, "Of two muscles or of two parts of a muscle, that which is nearer the head end of the body tends to be supplied by the higher, that which is nearer the tail end by the lower nerve. Of two muscles that nearer the long axis of the body tends to be supplied by the higher, that which is nearer the periphery by the lower nerve. Of two muscles that which is nearer the surface tends to be supplied by the higher, that farther from it by the lower nerve." He also points out that muscles which cause the same movement are not always supplied by the same nerve root. The action of the two pronators is indistinguishable, but the teres is supplied by the 6th root, the quadratus by the 8th and 1st dorsal. The 1st dorsal root was not found to send any filaments into the hand, the 2nd dorsal root is not mentioned as a constituent of the human plexus. Of the two "Laws" the first is I believe the earliest statement of an important truth.

Langley in the course of a paper[2] on the distribution of the sweat nerves of the foot of the cat refers to the movements produced in the hind limb of the animal by excitation of the roots of the lumbo-sacral plexus: he approaches the subject with a desire to ascertain whether the amount of variation, which he found to be considerable in the distribution of the sweat nerves (sympathetic system) has a correlative in the distribution of the nerves to the skeletal muscles of the limb. Like Kronenberg, Eckhardt, and Peyer, he found that excitation of the same nerve root does not always produce quite the same movements in the limb. Like Kronenberg, Eckhardt, and Herringham, he found that the proportion of contribution by

[1] *Proc. Roy. Soc.* Vol. XLI. p. 440.

[2] This *Journal*, Vol. XII. p. 366. September, 1891.

individual roots to the limb plexus is variable, and that the muscular distribution varies with that variation. The variations in the root contributions to the lumbo-sacral plexus of the cat are figured and arranged by Langley into three classes. My own experiments on the cat were running concurrently with those of Mr Langley. As in one section of this paper when mentioning my own I shall have to refer to his observations again, I will not here repeat the epitome of the limb movements which he gives. It is to be noted that his results differ widely from those obtained in the cat by Bert and Marcacci, and resemble those obtained by Forgue and Lannegrace in cat and dog.

SECTION II.

METHOD EMPLOYED. LIMB MUSCLES.

In the several researches which have had for subject the motor functions of the anterior divisions of the individual spinal roots of the limb plexuses, the leg plexus of the mammal has been less studied than has the plexus of the mammalian fore-limb.

I have employed for observation the frog, rat, rabbit, cat, dog, and monkey (Macacus); the five first-mentioned types chiefly for the sake of comparing them with that last mentioned in the list.

To stimulate the individual nerve roots the spinal canal was laid open, the animal being deeply anæsthetised with a mixture of chloroform and ether. In the case of the upper lumbar roots usually the whole root, both anterior and posterior divisions of it, was ligated, and cut through close to its point of transit across the dural sheath. By careful dissection it was freed to a considerable distance from the cord and lifted by a thread well up in the canal and drawn between well sheathed platinum electrodes (two mm. apart). In the case of the upper sacral and lower lumbar nerve roots the dural sheath of the cord having been laid open, the posterior roots were cut through, and the anterior rootlets were followed in one or more bundles to near the point of their exit beside the anterior column of the cord; to do this satisfactorily often involved the removal of a short length of the spinal cord. In following the rootlets from their point of exit from the dural sheath a loop of silk was in the earlier experiments slipped round the bundle of rootlets near the point of exit, and then pushed gradually up toward the cord; fine but tough threads of fibrous tissue tie the root filaments down, and this plan requires considerable care in avoiding damage to the root filaments. The connective tissue threads hinder the easy travelling of the loop, and it is better, because involving less risk of damage to the nerve fibres of the root bundles, to separate and follow up the bundles with a little polished metal hook. When followed to the point of their origin from the cord isolated bundles of rootlets five and six centimetres long are easily obtainable: these ligated, cut by the scissors and with their upper ends lifted well out of the canal drawn between the points of platinum electrodes were employed for stimulation.

To stimulate the anterior roots of the upper lumbar nerves it is well to excise a sufficient length of the cord, carefully preserving the anterior rootlets, and to follow at the risk of a little hæmorrhage the root in its dural sheath for a short distance through the intervertebral foramen, otherwise the roots are too short to stimulate without risk of escape of current.

For excitation induction shocks in rapid series from the sledge inductorium (R. Ewald's pattern) were employed. The secondary coil was usually at a distance from the primary more than double of that at which the induced currents were perceptible on applying the platinum electrodes to the tongue. In the primary circuit a single 1 pint Daniell cell was used.

In many instances the spinal root to be investigated was excited from the cortex cerebri, the root being previously isolated by section of the spinal roots adjacent to it.

In the course of the experiments it became clear that frequency of individual variation, as regards the anatomical and physiological constitution of the efferent roots of the lumbo-sacral region, is sufficiently great to demand the recognition of a forward and a hindward class innervation for each muscle and each movement. There is a *forward* class of individuals in which the roots connected with the muscles and the movements lie further forward (headward) than do the roots connected with the same muscles and the same movements in a *hindward* type of innervation. Since reference to this distinction must constantly recur in this paper and is of fundamental importance for appreciation of the problems involved, it seems well to avoid periphrasis and misunderstanding by using in reference to it special terms. A plexus and its trunks and branches will therefore be referred to as *prefixed* if containing spinal root-filaments attached to the cord further forward (headward) than are the root-filaments entering the corresponding trunks and branches of a converse class of plexus which will be referred to conversely as *postfixed*[1].

Thus, in the frog there is a *prefixed* class of plexus for the hind limb, in which, for instance, the vii root, as well as supplying the antero-internal thigh muscles, supplies muscles in the leg. There is a *postfixed* class in which the leg muscles are supplied by the viii and ix roots only. The *postfixed* class as measured by this standard is the more usual. The preponderance of the one type may be merely because the above criterion, found convenient for distinguishing in any individual case the direction which variation has taken in it, headward or tailward, does not coincide with the mid point about which individual variation is in the species really oscillating. Indeed we have not as yet evidence to shew that in this instance variation is oscillating about a single *mean* or maximum of frequency of individual examples. If a Curve of Error, to follow the term employed by Galton, were constructed it might here exhibit two maxima, one either side of the mean point.

By *prefixed* and *postfixed* classes it is not intended to imply that in the range of individual variation no one type is more frequently exemplified than are others; it is only meant that so frequent is the variation and so few are the data at present before us that it is not certain that any one type is sufficiently predominant to warrant the selection of it as "the normal" one, and that therefore it is better to treat the composition of the plexus of the species as multiple and for convenience to divide it into classes. I have thought two classes, *prefixed* and *postfixed*, distinction sufficient to observe in the present description. As in the frog, so in the other animals employed, the *prefixed* and *postfixed* class of plexus have both been exemplified by individuals taken from each species.

Frog.

A determination of the muscles supplied by the 7th, 8th and 9th nerves, namely those nerves forming the sciatic nerve, was attempted as

[1] In a preliminary abstract of the results detailed in this paper (*Proc. Roy. Soc.* 1892) I employed instead of *prefixed* and *postfixed* the terms *preaxial* and *postaxial*, the axis referred to being of course the axis of the limb. These terms I had been in the habit of using in my laboratory notebook although I had always felt them to be somewhat clumsy for their purpose. After the publication of the preliminary abstract, Dr Tooth very kindly wrote drawing my attention to the want of clearness of the terms, and I have determined to replace them by the above.

long ago as 1849 by Eckhardt[1]. He used induced currents and he noted that the same anterior root does not always innervate exactly the same muscles.

On the frog my own experiments have been upon the 7th, 8th, 9th and 10th nerve roots.

Root vii. Excitation causes the limb to be flexed and slightly adducted at the hip joint. It produces also some contraction of the lower part of the abdominal wall. As subminimal stimulation is gradually increased to and beyond minimal efficiency the sartorius is the first muscle to contract, then the three adductors. Six experiments all gave this result. As to the share of this root in the nerve supply to the pre-tibial and post-tibial muscle groups of the leg, when the knee was fixed and the contractions of the two sets of muscles recorded separately but synchronously in the myograph, excitation of root vii (by tightening a thread ligature or by pinching with fine ivory forceps) gave in two of twelve experiments, contraction of the pre-tibial set, and in one of those cases a slight contraction of the post-tibial set as well. Hallstén has noticed with regard to the nerve supply of the gastrocnemius, that the muscle can sometimes be caused to contract by excitation of root vii, sometimes not[2].

The position assumed by the limb after section of the 8th and 9th nerves is, when the frog is supported from the axillae, semi-extension at hip, knee, and ankle with some adduction, and tilting so that the foot tends to be placed somewhat in front of that of the sound limb.

Root viii. Excitation causes the limb to be flexed at hip without obvious adduction; at knee extension, at ankle extension (straightening); little or no separation of digits but flexion of digits and metatarsus.

Passing from sub-minimal to efficient stimuli there is extension of knee, flexion of digits, extension of metatarsus, extension of ankle; the toes can be separated by this root.

Tested in myograph in the manner above stated root viii was found in all of ten experiments to supply both pre-tibial and post-tibial sets of muscles; the contraction was vigorous in each group (fig. 3, XXIII.). The muscles which the nerve most easily brings into play are apparently those on the dorsum of the foot. When the three other roots are divided leaving only root viii the limb assumes a characteristic attitude; flexion at hip, knee, and extension at ankle. On giving a small dose of strychnia

[1] *Zeit. f. Rat. Med.* vii. 306.
[2] *Arch. f. Physiol.* 1885, p. 167.

however it becomes evident that the limb *can* be straightened fairly and completely at all its joints.

When root viii is cut, leaving roots vii and ix, the movements that can be performed are:

at hip—extension good, flexion feeble;

at knee—flexion good, extension feeble;

at ankle—flexion good, but extension feeble;

the metatarsus can be extended; in the digits extension and separation are both good.

Root ix. Excitation causes

at hip—extension without adduction;

at knee—extension;

at ankle—extension (i.e. straightening); in digits separation and extension.

Passing from subminimal to efficient stimuli the first movement is flexion of the 4th digit, then flexion of all the digits, then flexion of ankle and extension of digits.

Testing in myograph as above root ix always gave contraction of both the pre-tibial and post-tibial muscles, but the contraction of the former was less than in reply to excitation of the viii (fig. 3, XXIII.). In one case the ext. l. quinti digiti contracted well to excitation of the ix, but not well to that of the viii.

The position assumed when this root alone is left to the plexus is semi-extension at hip, knee, and ankle. It is questionable whether the flexion at knee is fully perfect. In reply to reflex excitation a peculiar lash-like movement often occurs in the limb, running down it and ending with a flagellum-like sweep of the toes, especially of the quintus. The position assumed by the limb when nerve roots vii and viii were cut and root ix only untouched resembled closely that taken when root viii only remained intact: flexion at hip, knee, and extension at ankle. The extension of the foot is immediately removed by cutting the peroneal nerve just below the knee. The movements that can be performed with root ix alone intact are at hip—flexion good, extension feeble; at knee, flexion and extension; at ankle extension good, flexion not good.

10th nerve gives contraction round cloacal orifice.

In the experiments with excitation mechanical stimuli were generally used, all the roots of the sciatic cut and the frog being suspended by the arms or the hip and knee fixed in the myograph the whole nerve root (ant. and post. divisions together) excited by tying a ligature or pinching with forceps. The roots were not exposed in the spinal canal but by removal of coccyx and the flap of skin and muscle to each side of that bone.

It was noticed that, in the experiments on innervation of the pre-tibial and post-tibial sets of muscle, that in seven of the eight instances in which the 7th nerve did not supply the tibial muscles, that nerve appeared smaller than in either of the two cases in which that group was supplied from the 7th, while the 9th nerve was larger than in those cases and gave a greater contraction of the pre-tibial set of muscles than in the five other instances. In one case however in which the 7th nerve did not supply the gastrocnemius the nerve appeared quite as large, perhaps larger than in any other instance. It thus appears that, in the *prefixed* class of the frog, which may be characterised by the motor fibres for the tibial muscles being contained in the 7th nerve, the 8th nerve root is usually obviously larger than in the *postfixed plexus,* but is not always so.

Not very rarely I have found the 6th root give quite a large branch to join the 7th, which receives it about half way between the spinal column and the point of formation of the sciatic trunk. In one of these cases the 6th root was excited mechanically and gave twitching in the rectus femoris anticus. The branch is not mentioned in the descriptions of the plexus by Deman, and by Ecker.

Cat.

The results I have obtained have not been uniform in this type; less so indeed than in the frog. In both species there appears to be a *prefixed* type, and a *postfixed* type of origin of the plexus; that is to say the nerve fibres which supply a certain muscle or group of muscles leave the spinal cord in some individuals higher up or lower down than they do usually, and this to such an extent that these fibres belong to a nerve root higher, or a nerve root lower in some individuals than in others. This fact several times pointed out by various observers has in the case of the cat been quite recently adverted to by Langley[1]. That anatomical variations in the sizes of the branches which the spinal nerves furnish to the lumbo-sacral plexus, go hand in hand with physiological variation, my own experiments and dissections have shown in accord with the results already mentioned by Langley.

The *postfixed* class of plexus.

The more usual in my experiments including 17 out of 27

[1] This *Journal*, vol. XII. p. 366.

individuals, one of which had twelve pairs of ribs, one fourteen pairs, the rest thirteen pairs.

1st lumbar. Contraction of abdominal wall; slight inward rotation of thigh, with slight flexion at hip.

2nd lumbar. Strong contraction of lower part of abdominal wall, slight flexion at hip.

3rd lumbar. Strong contraction of lower part of abdominal wall, flexion at hip with slight adduction. (Movement in round ligament, vas deferens, and bladder.)

4th. Contraction of lower part of abdominal wall, strong flexion at hip with adduction, rotation inward of thigh; slight extension at knee. (Movement in round ligament, vas deferens, and bladder.)

5th. Strong flexion at hip with strong adduction, slight extension at knee, no movement of foot. (Movement in bladder.)

6th. Slight extension at hip with slight adduction, strong extension at knee, flexion at ankle, with extension of toes.

7th. Extension at hip, and extension at knee, extension at ankle, toes extended and separated, claws unsheathed.

8th. (1st sacral), slight extension at hip, slight flexion at knee, strong extension at ankle, separation of digits, unsheathing of claws. (Protrusion of anus with closure of orifice; perinæum pushed down; constriction of orifice of vagina, tail abducted; emission of urine.)

9th. (2nd sacral), slight flattening of buttock and thigh (in two instances only). Interosseous flexion of digits. (Tail drawn to side stimulated; closure of anus; constriction of orifice of vagina; emission of urine.)

10th. No movement in limb. (No movement of anus; emission of urine; root of tail toward side stimulated.)

The *prefixed* class of plexus.

2nd lumbar. Strong contraction of lower part of abdominal wall, rotation inward, and flexion at hip.

3rd lumbar. Strong contraction of lower part of abdominal wall, flexion at hip with slight adduction? rotation inward. (Movement in round ligament, vas deferens, and bladder.)

4th lumbar. Contraction of lower part of abdominal wall, strong flexion at hip with strong adduction ? slight extension at knee. (Movement in round ligament, vas deferens, and bladder.)

5th lumbar. Slight extension at hip, with adduction, extension at knee ? extension at ankle. (Movement in bladder.)

6th lumbar. Strong extension at hip, extension at knee, flexion of ankle with extension of toes, claws unsheathed, toes separated.

7th lumbar. Strong extension at hip, slight flexion at knee, flexion at ankle, eversion of foot, extension of digits, unsheathing of claws, separation of digits. (Root of tail drawn towards side stimulated. Slight constriction of anal orifice.)

8th sub-thoracic (1st sacral). Slight extension at hip, and flexion at knee; extension at ankle. Separation of digits with flexion of the proximal and extension of terminal phalanges. (Protrusion of anus, with closure of it; root of tail drawn to side stimulated; contraction of vaginal orifice; emission of urine.)

9th sub-thoracic (2nd sacral). No movement in muscles of limb. (Slight protrusion and constriction of anal vaginal orifices; tail drawn toward side stimulated; emission of urine.)

10th sub-thoracic (3rd sacral). (No movement of anus, tail drawn toward side stimulated; emission of urine.)

11th, 4th. (No movement of anus, root of tail drawn to side away from side stimulated.)

12th. (Post. part of tail drawn toward side stimulated.)

13th. (Tip of tail toward side stimulated.)

In all animals used the plexus was sufficiently dissected after experimentation to examine at least on one side its construction with reference to the size of the branches contributed to it by the roots. The 4th and 8th nerve roots especially were examined closely, as I had been early led to associate the different results of excitation with difference in the size of these nerve roots; some dissections were not however carried further than to shew that in my *prefixed* type the contribution to the plexus from the 4th sub-thoracic nerve root was not so small as in the *postfixed* type, whereas in the case of the contribution to the plexus from the 8th sub-thoracic it was smaller than in the *postfixed* type.

I was not aware at the time of making the dissections that dissections were being made by Mr Langley, and on becoming so I sent to him two of the outlines I had drawn from my own preparations. One I considered a fair example of the origin of the plexus in my *prefixed* class, the other of its origin in my *postfixed* class. Mr Langley kindly compared them with his own drawings, and in his paper on the course of the sweat nerves to the foot of the cat mentions them as belonging broadly speaking to his classes III. and I. respectively. So that the anatomy and the two classes of results above mentioned may be compared with and will be seen to be in accord with those obtained by Langley.

I have only thrice made observations on the effects of excitation of lumbo-sacral roots of the dog: the results obtained agreed with the results obtained with the *prefixed* class of the cat; two of the dogs in question were found on dissection to possess only twelve pairs of ribs instead of the more usual thirteen, but in one of these there were eight lumbar vertebræ, and the transverse processes of the highest lumbar were larger than is normal.

Distribution of the Spinal roots to Muscles in Cat.

4th. pectineus; ilio-psoas; sartorius; superior rectus; vastus internus; rectus inferior and adductor longus. Bladder.

5th. ilio-psoas; rectus superior; sartorius; vastus internus, vastus externus, rectus inferior, crureus, gracilis, adductors—apparently all of them. Bladder.

6th. psoas; vastus externus; crureus; subcrureus; vastus internus; adductor magnus; rectus inferior; rectus superior; gracilis; semimembranosus > semitendinosus; flexor longus digitorum; tibialis anticus. Extensor biceps, longus digitorum, peroneus and gastrocnemius (especially the outer head) not always.

7th. Peroneus lateralis longus, peroneus lateralis brevis inferior, et superior soleus, gastrocnemius, flexor longus digitorum. Tibialis posticus, tibialis anticus, extensor longus digitorum, semitendinosus, semimembranosus, biceps, sometimes adductor magnus in part, sometimes the intrinsic flexors of the plantar region, gluteus. Sphincter ani sometimes.

8th. Soleus, gastrocnemius, peroneus lateralis. Intrinsic muscles of the plantar region. Biceps, semitendinosus, sometimes semimembranosus. Sphincter ani, sphincter vaginæ. Bladder.

9th. Intrinsic muscles of the plantar region (sometimes), sacrococcygeus superior. Soleus, vastus longus, and gluteus maximus (rarely), sphincter ani, sphincter vaginæ. Bladder.

10th. Sacrococcygeus. Bladder.

Monkey (Macacus rhesus).

Turning now to Macacus rhesus the following results are based on observations more numerous than those made on the other types.

In Rhesus the pairs of ribs are 12 in number; in two instances only in seventy-three specimens examined I have found thirteen ribs. The lumbar vertebræ are seven in number. In each of the two instances in which an extra pair of ribs existed the number of lumbar vertebræ was reduced to six. In one of those instances the small extra ribs were of very unequal size. In one instance the number of vertebræ between the lowest bearing ribs and the highest articulating with the ilia was six instead of seven, although there were only 12 pairs of ribs and the number of sacral vertebræ was as usual three. The peculiarities of this specimen will be referred to subsequently.

The arrangement and nomenclature of the muscles and muscular nerves of the lower limbs are in Macacus rhesus so similar, broadly speaking, to those obtaining in human anatomy that there is little need for special description here. A few points of difference do however require mention. Neither Macacus rhesus nor M. sinicus possesses a musc. peroneus tertius. The upper part of the biceps cruris is very large, and relatively much larger than in man. Gluteus maximus is flat and thin. The pectineus muscle receives no branch from the obturator nerve, at least I have never succeeded in finding an instance of it although I have frequently sought for it; its supply is from the anterior crural. A psoas parvus is quite usually present. The gracilis is relatively very large. The two tendons of insertion of the tibialis anticus are much more distinct and separate from one another in Macacus than in man. I have often found a peroneo-tibialis present. The abductor hallucis in man occasionally sends a slip to the base of the first phalanx of the 2nd digit; in Macacus rhesus and sinicus this slip is very large, distinct, and constant, forming in fact a separate muscle which I have never found wanting. A well-developed adductor hallucis is present. In Rhesus the plantar interossei adduct toward a line in the middle digit, the dorsal abduct from the same line. There is in Macacus frequently a communication between the external saphenous nerve and the external plantar nerve, above the heel deep to the tendo Achillis, and this branch of communication contains motor fibres to the intrinsic muscles of all the digits (Pl. XXI. fig. 7). Even at the top of the thigh the sciatic nerve consists of three separate divisions, as in the Cat. The largest of the three is the internal popliteal trunk, the next the external popliteal, the smallest from its distribution I have been accustomed to call the "hamstring" nerve. In Rhesus the movements of the hind limb are extremely free and extensive; the tail is short and stumpy and not so mobile as in many species.

Method of Examination by Minimal Excitation.

The method of analysing the distribution of the fibres of the motor roots by ascertaining what muscles contract when the fine filaments constituting the roots are individually excited by minimal electrical stimuli is very satisfactory in some respects. It probably enables one to say which muscle receives the larger number of the fibres composing the filament excited, if the various muscles supplied by the filament are all of about the same physiological quality, as frequently is the case. But it is to be remembered that as a muscle of large mass receives a larger number of fibres than another of smaller mass but of the same quality, so where the outflow of fibres to the two muscles overlap, the fibres to the larger muscle may preponderate in all the filaments that go to the two muscles, and the larger muscle may reply under accurately minimal stimulation of each of the root filaments and mask the supply to the muscle which is smaller. Again, very small muscles are, on account perhaps of the very smallness and lightness of the parts which they move, capable of giving visible movement and visible shortening with greater ease than some large ones. Thus, for instance, analysis by use of minimal stimuli of such root filaments as those of the 8th and 7th sub-thoracic roots which contain, among other interlapping outflows, the interlapping outflow of motor fibres to short flexor of the hallux and the sural triceps are likely to be misleading, because the mass of the two muscles supplied by the same filaments is very different, because resistance offered to movement by the great toe at the metatarso-phalangeal joint is very different from that offered by the whole foot at the ankle joint, and because the physiological quality of the two muscles is different, as evidenced among other facts by the much longer time which the sural triceps remains excitable after death. The method possesses however an advantage in guarding somewhat against mistakes due to escape of derivation of the currents used for excitation. Control observations are however a preferable safeguard in that difficulty. Analysis by means of minimal stimuli suffers from the want of certainty that the minimal stimulus employed is exerted fairly on the whole field of constituent fibres, and from the fact that a very slight inequality of distribution may make the difference between minimal and subminimal, efficient and inefficient, appreciable result and inappreciable. Also the results obtainable by it are absolute for the individual only, on account of the variable relation of the nerve root to the nerve trunks. Keeping the imperfection of the method in view I used it very frequently at the beginning of the experiments, usually combining it with the section of various peripheral nerve trunks.

The following list is compiled from the results of three experiments (Expts. 6, 15 and 21) which gave fairly similar results in three young female rhesi, in each of which the plexus was of the *postfixed* class. Other experiments as above mentioned did not agree so closely with these or with themselves as did the subjoined. For the before-mentioned reasons, although the appended list is given and its results may be interesting, yet they are of little value as representative of absolute specific localisations in the cord but rather merely of the relative positions and sequences that tend frequently to occur in it.

No. of nerve root.	No. of rootlet in root.	Name of muscles contracting on minimal excitation.	No. of Expt.
3rd	1	cremaster, then psoas and pectineus	15. 21. 6
	2	cremaster, then psoas and pectineus	15. 21. 6
	3	cremaster, then psoas and pectineus	15. 6.
	4	psoas and pectineus*, then cremaster and sartorius (upper part)	15. 21.
	5	psoas and pectineus*, then cremaster and sartorius	15. 21.
	6	psoas and pectineus*, then sartorius	15. 21.
	7	pectineus*, then sartorius	15. 21. 6
	8	pectineus*, then sartorius	15. 21. 6
4th	1	pectineus*, then sartorius and gracilis	15. 21. 6
	2	sartorius, then pectineus and gracilis	15. 6.
	3	sartorius, then pectineus, gracilis and rectus	15. 6.
	4	sartorius, then gracilis and rectus	15. 6.
	5	sartorius, then gracilis and rectus	15. 6.
	6	rectus, then gracilis	15.
	7	rectus and gracilis, then vastus internus	15. 21.
	8	rectus and gracilis, then vastus internus	15. 21.
	9	rectus and gracilis, then vastus internus	15. 21.

* Not altered by section of the obturator nerve in the pelvis.

5th	1	rectus and gracilis, then vastus externus, and internus	15. 21. 6
	2	rectus and gracilis, then vastus externus and internus	15. 21. 6
	3	gracilis and vastus externus, then vastus internus	15.
	4	gracilis and vastus externus, then tibialis anticus	15. 21.
	5	gracilis and vastus externus, then tibialis anticus	15. 21.
	6	tensor vaginae femoris, then gracilis and vastus externus	15.
	7	gracilis and vastus externus, then pre-tibial muscles	15. 21. 6
	8	gracilis and vastus externus, then pre-tibial muscles	15. 21. 6
	9	adductor magnus and semimembranosus, then pre-tibial muscles	15. 21. 6

	10	adductor magnus and semimembranosus, then pretibial muscles	15. 21. 6
	11	adductor magnus and semimembranosus, then pretibial muscles	15. 21. 6
6th	1	tibialis anticus, then peroneus longus	15. 6.
	2	tibialis anticus, then peroneus longus	15. 6.
	3	tibialis anticus, then peroneus longus	15. 6.
	4	tibialis anticus, then flexor longus hallucis	15.
	5	tibialis anticus, then peroneus longus	15. 6.
	6	tibialis anticus, then flexor longus hallucis	15. 21.
	7	tibialis anticus, then peroneus longus and flexor longus hallucis	15. 21.
	8	tibialis anticus and flexor longus hallucis, then flexor perforans	15.
	9	tibialis anticus and flexor longus hallucis, then flexor perforans	15. 21.
	10	tibialis anticus and flexor longus hallucis, then peroneus longus	15. 21. 6
	11	flexor longus hallucis, then tibialis anticus and peroneus longus	15. 21.
	12	flexor longus hallucis, then tibialis ant. and peron. longus	15. 21. 6
7th	1	flexor longus hallucis and flexor perforans	15. 21. 6
	2	flex. longus hallucis and flexor perforans or tibialis anticus, or peron. longus	15. 21. 6
	3	flexor longus hallucis, then tibialis posticus	15.
	4	flexor longus hallucis and tibialis posticus	15. 21. 6
	5	flexor perforans and peroneus brevis	15.
	6	peroneus brevis, then tibialis posticus	15.
	7	peroneus brevis and gastrocnemius	15. 21.
	8	peroneus brevis and gastrocnemius	15. 21.
	9	intrinsic flexor* of hallux, then gastrocnemius	15. 6.
	10	intrinsic flexor* of hallux, then gastrocnemius	15. 6.
	11	intrinsic flexor* of hallux and minimus, then semitendinosus	15. 21. 6
	12	intrinsic flexor* of hallux or minimus, then semitendinosus	15. 21. 6
8th	1	intrinsic flexor* of hallux, then outer head of gastrocnemius	15. 6.

	2	intrinsic flexor* of hallux, index or quintus, then biceps and anus	15. 21. 6
	3	intrinsic flexor* of hallux, index or quintus, then biceps and anus	15. 21. 6
	4	intrinsic flexor* of hallux, index or quintus, then biceps and anus	15. 21. 6
	5	intrinsic flexor* of hallux, index or quintus, then anus	15. 21. 6
	6	intrinsic flexor* of hallux, index or quintus, then other digits and anus	15. 21. 6
9th	1	anus and intrinsic flexor* of hallux or quintus, then other digits	15. 21. 6
	2	anus and intrinsic flexor* of hallux or quintus, then other digits	15. 21. 6
	3	anus and intrinsic flexor* of hallux or quintus, then other digits	15. 21. 6

* This flexor action was always accompanied by adduction. After the external plantar nerve had been cut through it was unaccompanied by any marked adduction. After section of the internal plantar nerve it persisted very much as before. When exposed to inspection it could be seen that the adductor and other intrinsic muscles of the toe were all in action. I could not isolate the individual muscles by modifying the strength of the excitation; the point of minimal excitation appeared to be the same for all of them.

Excitation of isolated roots or rootlets by currents of medium strength.

A more just estimation of the functions of an efferent root is obtainable by using currents of intensity sufficient to ensure fairly equal excitation of all the component nerve fibres in the spinal root or rootlet. By such excitation it soon becomes evident that in Macacus a *prefixed* class and a *postfixed* class of plexus formation has, just as in the frog and cat, to be distinguished. As in the frog and cat, the distribution of the same spinal root of the plexus is not in all individuals the same. The fact is evidenced not only by excitation experiments, but also by severance experiments. When one motor spinal root of the limb plexus has been isolated by section of the adjacent ones the degree of movement left is not always the same for the same root in different individuals. For instance in two young Rhesi in which the seventh cervical root to the brachial plexus had been isolated in the same way (by section of the 4th, 5th, 6th and 8th cervical and the highest two thoracic roots) the power of grip of the hand was strikingly different in the two individuals; the power of folding the thumb especially was dissimilar in the two; dissection revealed no difference in the extent of the experimental lesion. In the cat the *prefixed* and *postfixed* classes of innervation of the limb seemed to be pretty evenly balanced in frequency of occurrence, the *prefixed* class being rather the less usual of the two. In Macacus rhesus, again, there seems to be, judging from sixty-six experiments, a slight preponderance of *postfixed* type over *prefixed*. The upper lumbar roots do not appear to vary so much as do the lower and the sacral. I will state briefly the arrangement evidenced in the larger number (37) of the experiments.

Postfixed Class of plexus. (Pl. XX. fig. 1.)

Spinal roots and movements.

1st sub-thoracic root (1st lumbar). Retraction of abdominal wall. (Erection of hair.)

2nd. Retraction of lower part of abdominal wall. Drawing up of testicle. Slight flexion at hip. (Erection of hair; movement in round ligament, vas deferens, and bladder.)

3rd. Contraction of lower part of abdominal wall, drawing up of testicle (stronger than with 2nd). Flexion at hip, slight flexion at knee, slight rotation outwards of thigh. (Erection of hair; movement in round ligament, vas deferens, and bladder.)

4th. Drawing up of testicle (slight)? Contraction of lower part of abdominal wall. Flexion at hip, with adduction of thigh extension at knee, slight rotation outwards of thigh. (Movement in bladder.)

5th. Flexion at hip, with adduction of thigh, extension at knee, drawing up of inner edge of foot, with slight flexion[1] at ankle, and slight extension of hallux. Section of this nerve root alone causes no obvious paralysis of the limb, although the limb when at rest, the animal being held up under the arm-pits, droops more at the knee than does the limb of the sound side: the knee-jerk is however abolished.

6th. Extension at hip, with adduction of thigh, weak flexion, or even extension, at knee, flexion at ankle, lifting of inner edge of foot, extension of toes with adduction of hallux.

7th. Extension at hip, flexion at knee, extension at ankle, tilting of outer edge of foot, flexion of digits with strong adduction of hallux, depression of root of tail. Slight rotation outward of the thigh.

8th. Slight rotation outward of the thigh, extension at hip, flexion at knee, extension (very strong) at ankle. Strong flexion and adduction

[1] Cf. *Quain's Anatomy*, 10th Ed. Vol. II. pt. 2, by G. D. Thane, pp. 191 and 273; also Gowers' *Dis. of the Nerv. System*, Vol. I. p. 34.

of hallux, flexion of digits in "interosseal" position. (Contraction of anus and vaginal orifice; root of tail depressed and drawn to side stimulated; emission of urine; erection of penis.)

9th. Slight rotation outward of the thigh. Flexion and adduction of hallux; flexion of digits. (Perineum pushed down. Contraction of anus and of orifice of vagina; abduction of root of tail toward side stimulated; emission of urine; erection of penis.)

10th. (Abduction of root of tail toward side stimulated; emission of urine.)

11th. (Proximal two-thirds of tail drawn toward side stimulated.)

12th. (Distal half of tail drawn toward side stimulated.)

13th. (Tip of tail drawn toward side stimulated.)

Although it is not possible in any one experiment to expose and isolate the numerous separate muscles composing the musculature of the whole limb, and so to determine individually their actual and active participation in the above-mentioned movements, still it is possible in the course of a series of experiments to expose a certain number of individual muscles in each experiment. All in the following list have been actually examined in this way by inspection and by touch; many by the myograph as well, isometric records more frequently than isotonic being taken.

Spinal roots and muscles. (Pl. XXI. fig. 8.)

1st sub-thoracic (1st lumbar) root. Quadratus lumborum, psoas parvus, psoas magnus, external oblique, internal oblique, transversalis.

2nd sub-thoracic. Quadratus lumborum, psoas magnus, psoas parvus, cremaster, external oblique, internal oblique, transversalis.

3rd sub-thoracic. Psoas magnus, psoas parvus, cremaster, iliacus, external oblique, transversalis (the lower part only of the three latter) pectineus, adductor longus, sartorius.

4th sub-thoracic. Psoas magnus, iliacus, pectineus, the adductor longus, gracilis (probably the rest of the adductor mass), sartorius, vastus internus, vastus externus, crureus, rectus fem. (slight), obturator externus.

5th sub-thoracic. Psoas magnus (small prevertebral part of), gracilis, adductor longus (slight), tensor vaginæ femoris, rectus femoris, vastus internus, vastus externus, crureus, sartorius (slight), tibialis anticus (only slightly), extensor hallucis (very slight), extensor longus digitorum (very slight), peroneus longus (very slightly).

6th sub-thoracic. Part of adductor magnus, tibialis anticus, extensor longus digitorum, extensor hallucis, peroneus longus (> peron. brev.), peroneus brevis, short (intrinsic) extensors of the digits, abductor minimi digiti, gastrocnemius (both heads, but slight), popliteus, tibialis posticus, flexor longus digitorum, long flexor of the hallux, soleus (slight), semimembranosus, plantaris, semitendinosus, biceps, upper part of pyriformis; quadriceps extensor cruris (rarely), gracilis (near knee, rarely).

7th sub-thoracic. Adductor magnus, semitendinosus, semimembranosus, tibialis anticus, extensor longus digitorum, ext. propr. hallucis, peroneus brevis (> peroneus longus), peroneus longus, plantaris, popliteus, gastrocnemius (both outer and inner heads), tibialis posticus, flexor longus digitorum, soleus, long flexor of the hallux, short extensor (intrinsic extensor) of the digits and hallux, short and accessory flexors (intrinsic flexors) of the digits and hallux, abductor minimi digiti, abductor hallucis, adductor hallucis interossei and lumbricales. Deeper part (?) of sphincter ani. Large part of pyriformis, obturator internus. Quadratus femoris and two gemelli, gluteus medius, gluteus maximus.

8th sub-thoracic. Biceps, semimembranosus, semitendinosus, gluteus maximus, gastrocnemius both heads, soleus, tibialis posticus, flexor longus digitorum (slight), flexor long. hallucis. Abductor hallucis, abductor minimi digiti. Short and accessory flexor of the digits and hallux, adductor of the hallux. Interossei and lumbricales, superficial part of sphincter ani. Sphincter vagina, small part of pyriformis. Obturator internus, quadratus femoris and the two gemelli.

9th sub-thoracic. Short flexors of the digits and hallux. Adductor of the hallux. Interossei and lumbricales. Sphincter ani. Sphincter vaginæ. Obturator internus, part of gluteus maximus.

In accord with the above description a number of incidental observations were also obtained of which the following are examples.

All the structures about the ankle except the main blood-vessels, the bones and deep ligaments and the anterior tibial nerve severed. Anterior root of 6th sub-thoracic exposed, ligated, cut and stimulated by pinching, then by induced currents. Both forms of excitation elicited opening and extension of toes, with adduction of hallux. Similar stimulation applied to 7th root gave similar but not so marked reply; excitation of 5th root elicited no movement in foot although strong currents were ultimately used for excitation. The short extensors of the digits, and the abductor hallucis therefore, receive motor fibres through the 6th and 7th sub-thoracic nerves.

All structures about ankle severed except the main blood-vessels and the posterior tibial nerve. Anterior root of 9th nerve (2nd sacral) exposed in the spinal canal, isolated, ligated, cut, and stimulated by tying threads tightly round its end, and by induced currents. The excitation elicited forcible folding (flexion) of digits with adduction and flexion of hallux. The anterior root of the 8th nerve gave the same result. The anterior root of the 7th gave a similar but less forcible action.

All structures about ankle severed except the tendon of the flexor longus digitorum. Excitation of the anterior root of the 7th sub-thoracic in the spinal canal gave flexion of all the toes, especially perhaps of the hallux. Excitation of the 6th gave a similar but weaker flexion.

All the structures about ankle severed except the tendons of the extensor longus digitorum and extensor proprius hallucis. Excitation of anterior root of the 6th in the spinal canal gave extension and adduction of digits and hallux.

All structures about the ankle severed except external plantar nerve. Excitation of the anterior root of the 9th in the spinal canal, but not of the 6th, gave flexion (but not very powerful) of the digits excepting hallux.

The 3rd and 4th, and the 6th and the 7th anterior roots divided on the left side. The central end of the divided posterior root of the 4th nerve excited in the central canal; the reflex movement obtained was a smart extension at ankle joint; therefore the 5th anterior root gives besides extension of the knee, extension of the ankle.

Excitation of the 6th anterior root gives (v. supra) slight flexion at knee, flexion at ankle, tilting of outer edge of foot, and extension of toes with adduction of hallux, but after the external popliteal has been cut through gives flexion at knee and hip (the inner hamstrings and the adductors obviously contracting at the same time), extension at ankle, flexion of digits and hallux at all joints, the flexion is not usually of great force, it persists after section of the plantar. Excitation of the 6th anterior root of the opposite side, which had been giving the same reply as that at first given by its fellow, gave, after section of the internal popliteal nerve, strong flexion of the foot, questionable extension of the digits, slight straightening and adduction of the hallux; or sometimes very strong extension of the digits and hallux with adduction of the latter. In either case, i.e. whether strong or weak, the extension of the digits and hallux with adduction of the latter persists after section of the anterior tibial at the ankle.

The right and left lumbar roots exposed in the spinal canal; the right external popliteal nerve divided, the left internal popliteal nerve divided, both in the ham; the left anterior tibial and the right external and internal plantar nerves divided at the ankle. Upper part of "motor" cortex exposed right and left. Extension of the right knee obtained from left cortex close behind Schäfer's sulcus *x*. The right-hand 3rd and 4th roots cut across. Extension of knee (with ? slight flexion of toes) still obtained. Right 5th root divided. Extension of knee still obtained from cortex, but much feebler. Extension of knee obtained from right cortex near top of precentral gyrus; section of 3rd, 4th, and 5th left-hand lumbar roots; feeble extension of left knee still obtained. Removal of cord from 3rd to 7th lumbar segment. Excitation of anterior root of right 6th (about 40 mm. long) gives extension of knee (somewhat feeble) with strong flexion of all digits and extension of the ankle (due to action of deep post-tibial group chiefly, it being questionable whether the gastrocnemius and soleus are in action at all). Excitation of anterior root of left 6th lumbar gives extension of knee accompanied by extension of digits and flexion of ankle, the peroneus longus being in strong contraction but the peroneus brevis only questionably. In four individuals only have I seen extension of the knee result from excitation of the 6th sub-thoracic root.

The right and left lumbosacral roots exposed in the spinal canal; the right and left external popliteal nerves divided below head of fibula; at each ankle the tendo Achilles and the tendons of the flexor longus hallucis and digitorum divided; upper part of "motor" cortex (right and left) exposed. Excitation of right cortex behind top of sulcus centralis gives opposition of hallux and flexion of digits. 9th sub-thoracic root of left side cut through; excitation of cortex gives same result as before. 8th root then cut; cortical effect as before. 7th root then cut, cortical excitation gives no movement of digits. Left cortex excited at top of sulcus centralis gives opposition of hallux and flexion of digits. 7th sub-thoracic root cut on right side, cortical result as before; 8th root cut, cortical result as before, but weaker. 9th root cut through, no movement of digits or hallux on cortical excitation.

Excitation of the 7th anterior roots when they, as usual, are giving (v. supra) flexion at the knee, extension at ankle, tilting of outer edge of foot, and flexion of digits with strong adduction of hallux, after section of the external popliteal nerve causes strong flexion of hallux and digits at all joints with adduction, extension at ankle with tilting upward of inner edge of foot, flexion at knee, both outer and inner hamstrings contracting. The flexion of the digits and hallux and the adduction of the latter are not sensibly altered by section of the plantar nerves. Excitation of the 7th anterior root gives, after section of the internal popliteal nerve, strong extension of toes, especially at metatarsal joints and straightening with slight adduction of the hallux, strong flexion of ankle, tilting of outer edge of foot, strong flexion of knee, and sometimes extension of thigh.

Excitation of the 8th anterior root in spinal canal, which had been giving as usual extension at ankle with obvious contraction of the superficial calf muscles, flexion of the digits, and flexion and adduction of the hallux, with some flexion at the knee by action of the biceps especially, gave on the plantar nerves being cut through at their origin the same movement as before except for weakening of flexion of digits and hallux, and of adduction of the hallux.

Excitation of the 8th anterior root which had as usual caused flexion of the digits and hallux with adduction of the latter continued to do so well after section of both plantar nerves, but with modification of the character of the adduction and flexion.

Excitation of the 8th anterior root after section of internal popliteal nerve at the edge of the pyriformis gave flexion of the knee with tightening of the biceps tendon, tilting up of outer edge of the foot, and no other movement in the leg.

For reasons already given the individuals (29 out of my series) not conforming fairly to the plexal arrangement just described, I have considered it well to treat *en bloc* as forming another class and to place together as a second experimental series.

Prefixed Class of Plexus. (Pl. XX. fig. 2.)

Spinal roots and movements.

1st. Retraction of abdominal wall (near umbilicus in front). (Erection of hair.)

2nd. Retraction of lower part of abdominal wall; flexion of hip, with some eversion; drawing up of testicle (stronger than with 3rd). (Erection of hair; movement in round ligament, vas deferens, and bladder.)

3rd. Retraction of lowest part of abdominal wall; drawing up of testicle, flexion at hip, with marked rotation of thigh outwards and some adduction; some extension of knee. (Erection of hair; movement in round ligament, vas deferens, and bladder.)

4th. Flexion at hip; extension at knee; adduction of thigh; eversion of thigh. (Bladder.)

5th. Flexion at hip; extension at knee rarely flexion; adduction; strong flexion at ankle; drawing up of outer edge of foot; flexion of hallux and digits.

6th. Extension at hip; adduction of thigh; strong flexion at knee, extension at ankle; rotation of leg inwards; lifting of outer edge of foot; flexion of digits and hallux at terminal joint, with (sometimes) adduction. (Slight retraction of anus.)

7th. Extension at hip, with slight rotation outward of the thigh; flexion at knee, extension at ankle; rotation of leg outwards; flexion of digits and hallux, with adduction of hallux, sometimes abduction of hallux and minimus. (Depression and abduction of root of tail; protrusion and feeble constriction of anus, rarely of vaginal orifice also.)

8th. Extension at hip, with slight rotation outward of the thigh; flexion at knee; extension at ankle; strong flexion and abduction of hallux; flexion of digits in "interosseous" position. (Closure and protrusion of anus; root of tail drawn to side stimulated and depressed; perineum pushed down; constriction of vaginal orifice; emission of urine; erection of penis.)

9th. (Abduction of root of tail, which is drawn toward the side stimulated; constriction of vaginal orifice, and of anus—occasionally feeble; emission of urine; erection of penis.)

10th. (Proximal half of tail drawn toward side stimulated; emission of urine.)

Spinal roots and muscles. (Pl. XXI. fig. 9.)

1st sub-thoracic (1st lumbar)

Quadratus lumborum	Internal oblique
Psoas parvus	Transversalis
External oblique	Psoas magnus

2nd sub-thoracic

Quadratus lumborum	External oblique
Psoas magnus	Internal oblique
Psoas parvus	Transversalis
Cremaster	

3rd sub-thoracic

Psoas, cremaster, iliacus	Adductor longus
External oblique	Sartorius (upper part especially)
Internal oblique (lower part only)	Vastus internus, and obturator externus slightly
Transversalis	Rectus femoris (upper part, slight)
Pectineus	

4th sub-thoracic

Psoas, iliacus
Pectineus
Adductor longus
Sartorius (lower part especially)
Vastus internus (> vastus externus)
Crureus

Obturator externus
Rectus femoris
Vastus externus
Gracilis
Adductor brevis
Adductor magnus

5th sub-thoracic

Gracilis
Vastus externus (> Vastus internus)
Rectus femoris
Vastus internus
Crureus
Adductor magnus
Tibialis anticus
Extensor longus digitorum
Extensor proprius hallucis
Tensor vaginæ femoris

Peroneus longus (slight)
Semimembranosus (slight)
Flexor longus hallucis (occasionally strongly)
Flexor longus digitorum (occasionally strongly)
Tibialis posticus (occasionally strongly)
Peroneus brevis (?)
Highest portion of pyriformis (?)

6th sub-thoracic

Tibialis anticus
Extensor longus digitorum
Extensor hallucis
Peroneus longus
Peroneus brevis
Extensor brevis digitorum
Gastrocnemius, external head (> internal head)
Gastrocnemius, internal head
Tibialis posticus
Flexor longus digitorum
Flexor longus hallucis
Semimembranosus (> semitendinosus)
Semitendinosus

Biceps (chiefly in deep portion)
Abductor hallucis
Flexor brevis digitorum
Abductor hallucis (slight)
Abductor minimi digiti
Soleus (slight)
Plantaris
Popliteus
Pyriformis
Gluteus medius
Quadratus femoris
Gemellus inferior
Gemellus superior
Gluteus minimus

7th sub-thoracic

Tibialis anticus
Extensor longus digitorum
Extensor proprius hallucis
Peroneus longus (slight and < Peroneus brevis)
Peroneus brevis
Gastrocnemius, external head
Gastrocnemius, internal head
Plantaris
Tibialis posticus
Flexor longus digitorum
Soleus
Flexor longus hallucis
Extensor brevis digitorum
Flexor brevis digitorum
Abductor hallucis
Abductor minimi digiti
Flexor accessorius
Flexor brevis hallucis
Flexor brevis minimi digiti
Adductor hallucis
Interossei and lumbricales
Obturator internus
Quadratus femoris
Gemelli superior and inferior.
Pyriformis (the larger part of, esp. the lateral part)
Deeper part of sphincter ani
Semitendinosus
Semimembranosus
Biceps
Adductor magnus (part of)
Popliteus
Gluteus medius
Gluteus minimus
Gluteus maximus
Sphincter ani

8th sub-thoracic

Biceps (> than semimembranosus)
Semitendinosus (> than semimembranosus)
Semimembranosus
Gluteus maximus
Gastrocnemius, internal head (> than external)
Gastrocnemius, external head
Soleus
Abductor hallucis
Flexor brevis digitorum
Flexor accessorius
Abductor minimi digiti
Adductor hallucis
Obturator internus
Quadratus femoris
Gemelli sup. et inf.
Pyriformis (small part, chiefly mesial)
Spincter ani
Sphincter vaginæ
Flexor brevis hallucis
Flexor brevis minimi digiti
Lumbricales and
Interossei

9th sub-thoracic

Sphincter vaginæ

In accord with this latter series stand also a number of incidental observations obtained in the course of other experiments of which the following are examples.

All structures about ankle severed except main blood-vessels and the posterior tibial nerve. Anterior root of 6th nerve exposed, isolated for 6 cm., ligated, cut, lifted and stimulated gives somewhat feeble flexion of digits with adduction and flexion of hallux. The anterior-root of 7th gave similar but more forcible action; so also anterior root of 8th. No movement in foot on exciting anterior root of 9th with even very strong currents, i.e. secondary at 12 cm.

All structures about the ankle severed except external plantar nerve: excitation of the anterior root of the 6th in the spinal canal gave flexion (but not powerful) of the digits except the hallux.

Excitation of the 8th anterior root in the spinal canal, which had been causing extension at ankle with obvious contraction of the sural triceps, flexion of the digits, and flexion and adduction of the hallux with flexion at knee, gave when the plantar nerves were cut through the same movement as before except for absence of flexion of digits and hallux, and instead of adduction of the hallux a slight parting of it from the other toes.

Lumbo-sacral roots exposed in canal. The internal popliteal nerve divided each side under the gluteus. Right and left "motor" areas exposed. At the ankle all the tendons on the front of the joint divided. Excitation of right cortex above Schäfer's sulcus *x* gives opening of digits. Left 9th root cut; excitation of cortex gives same result as before. 8th root cut, excitation gives same result as before. 7th root cut, excitation gives same result as before. 6th root cut, excitation no longer gives movement in foot.

Excitation of left cortex near sulcus *x* gives extension of digits. Then right 6th root cut, excitation gives a less (weaker) movement than before. Section of 7th root, excitation of cortex no longer gives any movement of digits.

Right and left "motor" areas exposed; also lumbo-sacral roots in the spinal canal. Tendons of right peroneus brevis attached to myograph, excitation of cortex in front of upper end of the central sulcus gives smart contraction. 8th root of left side cut, contraction as before to cortex. 7th root cut, contraction diminished. 6th root cut, contraction lost. Cortex on left side stimulated, reply from peroneus brevis obtained, tendon attached to myograph. Then 6th root of right side cut, cortical reply diminished. Then 7th root cut, cortical reply absent.

On three occasions contraction of the intrinsic muscles of the sole has been obtainable from two roots only, viz. the 8th and 7th, the 9th root in neither case causing any movement in the limb. One of the occasions referred to was that in which only 6 lumbar roots and vertebræ existed instead of the usual seven.

I have no reason to believe that my results obtained by excitation of isolated spinal roots, or their isolated filaments, in the spinal canal were vitiated by escape of current, because aware of the risk of such an accident my efforts during the experiments have been carefully directed to minimising such risk (1) by isolating the whole length of each root (sometimes a length six centimetres long), and lifting it well out of the depth of the wound on to the electrodes; (2) by using currents of weak strength, in most cases quite too weak to be felt by the tongue, and in most cases with the secondary coil twice as far from the primary as the point at which the current became perceptible to the tongue. They are moreover controlled by other observations. Control results were in a certain measure obtained as a matter of routine during the direct excitation experiments by noting the result obtained on mechanical stimulation of them by tightening one after another parallel loops of thread placed near together round the root at its cut end, the first tightening of course being the one nearest the cut end. The results of the mechanical stimulation although feeble, and in large muscles not easy to observe, in no instance disagreed with the effects of the electrical stimulation, but in every case was confirmatory of the electrical excitation. Often the mechanical excitation was used before the electrical, often after the electrical. In other control observations the ventral nerve roots immediately above and immediately below the one to be investigated were divided; a sufficient time was then allowed for degeneration to have play; and finally electrical excitation of various nerve trunks in the limb was employed. Five experiments were performed thus on Rhesus. Details of these may be given shortly. Much of the motor defect at first resulting proves transient.

The numbers given indicate in centimetres the distance of the secondary coil on the slide of the inductorium; they are noted here merely to serve as a rough guide to the relative condition of the various nerves, and in comparing with one another the numbers for the opposite sides of the body and for the same side of the body, it is to be remembered that as the experiment progressed, the nerves, owing to exposure and other unavoidable causes, were some of them not in condition for accurately contrasting their excitability. Still the numbers appear to have a significance the broad features of which seem unmistakable.

25, vi. Young female. The 3rd and 4th and the 6th and 7th sub-thoracic roots of the right side divided completely just distal to the ganglion, i.e. ventral and dorsal divisions of the root severed together.

26, vi. Movements of right limb obviously impaired, seemingly less so at ankle than at hip and knee; the clasp of the right foot is feeble. Knee-jerk brisker right than left.

14, vii. Movements in cage seem almost normal; holds side of cage better with left hallux than with right. Continued observation detects performance at the hip of flexion, and extension; at the knee of flexion (outer hamstring tightens very obviously both to inspection and to touch) and extension; at ankle, of flexion, and extension (latter weaker than left); in digits, of extension and flexion, latter weak.

10, viii. Obvious wasting of the anterior muscles of the right thigh, right calf, and of the inner hamstring mass. Knee-jerk is brisker right than left.

10.15 A.M. A.C.E. mixture administered; when anæsthesia has been obtained, anterior crural of right side is divided close below Poupart's ligament. Excitation of central end gives reflex on to adductor group of the thigh.

10.42. Excitation of distal end gives extension at knee. Branches of anterior crural exposed and distal ends stimulated.

10.54. Upper branch to sartorius; no contraction.

Branch to rectus femoris	contraction at 15.
,, ,, vastus externus and crureus	,, ,, 19.
,, ,, vastus internus and crureus	,, ,, 16.
,, ,, crureus	,, ,, 18.

11.16. External popliteal close below gluteus maximus exposed.
Central end gives reflex on to semimembranosus.
Distal end gives contraction in leg and foot.

11.28. Anterior tibial nerve. Distal end: contraction.
Musculo-cutaneous nerve. Distal end: contraction.

11.37. Distal ends of
a branch to tibialis anticus replies at 17. (Left side at 48.)
,, ,, extensor longus digitorum at 13. (Left side at 42.)
,, ,, extensor hallucis at 16. (Left side at 41.)

11.53. Distal end of anterior tibial nerve on front of right ankle gives opening of toes with extension at 28 cm.
Distal end of same nerve left side at same place gives good opening of toes at 48 cm.

12.7. Right nerve to peroneus longus: contraction at 24 (left at 46).
,, ,, peroneus brevis: ,, ,, 7 (left at 46).
(This result, not well in accord with my other experiments, was obtained in this experiment several times over at intervals during

the experiments, being repeated in order to test its reality; although the figures obtained varied somewhat the general features of the observation were constant, thus:

Peroneus longus at 12.11 = 27, at 12.33 = 25.
Peroneus brevis „ „ = 12, „ „ = 8.
at 12.48. = 24, at 1.14 = 22, at 1.15 = 23.
„ „ = 9, „ „ = 8, „ „ = 8.

Examined microscopically the nerve to brevis contained fewer sound fibres than nerve to longus).

Internal Popliteal.

12.35. Branch to external head of gastrocnemius, contraction at 23, (left at 49).
„ „ internal head, contraction at 30
„ „ soleus at 28 (left at 54).
„ „ tibialis posticus at 4 (left at 53).

12.55. Branch to flexor longus digitorum, feeble contraction at 26 (left at 48).
„ „ flexor hallucis at 21 (left at 57).

Hamstring nerve (3rd division of Sciatic trunk).

1.17. Excitation of central end gives reflex.
„ distal end „ contraction in hamstrings.
Branch to semimembranosus, contraction at 28 (left at 48).
„ „ and adductor magnus, at 32 (left at 47).
„ semitendinosus, contraction at 25 (left at 49).
Upper branch to biceps, contraction feeble at 22 (left at 53).
Lower „ „ contraction at 23 (left at 52).

1.54. Obturator nerve outside the obturator foramen.
Central end gave reflex on to psoas.
Distal end gave contraction in thigh.

1.59. Distal end of branch to adductor longus, contraction at 21.
„ „ gracilis, good contraction at 24, but the upper part of the muscle is obviously wasted.
branch to another part of the adductor mass, contraction at 18.
Branch to pectineus from anterior crural nerve, gives contraction feebly at 7, the muscle itself is obviously wasted.

On examination within the spinal canal it was found that the 5th root was intact, two roots above it and two below it being imbedded in fibrous tissue &c. When the dura mater had been opened it was found that excitation of the distal end of the divided rootlets of the 3rd and 4th and 6th and 7th nerves gave no detectable movement; excitation of the rootlets of the 5th nerve produced movement at the root of the tail. The 9th rootlets gave contraction in the tail. The 8th root was not excited because it was very adherent to the dura at one point.

The cord shewed ascending degeneration to the naked eye even at the top of the cervical region, this degeneration proceeding from the dorsal root of the 6th lumbar chiefly, shewing that the ganglion of the dorsal root of that nerve had been injured at the time of the first operation.

6, vi. 90. Young female. Ant. and post. roots of right 4th, 5th, 7th and 8th sub-thoracic nerves divided in the spinal canal.

8, vi. Keeps in sitting posture, reluctant to rise, but *can* erect itself fully. Knee-jerk absent right.

6, vii. Springs freely about cage, but left side always kept toward the wired part (used for climbing); from roof hangs as often by right as by left leg. Grasps fairly with right foot, better than animal operated on 25, vi. Jerk absent right.

8, viii. 90. Wasting of right anterior thigh muscles, of calf, and of outer hamstring. Knee-jerk absent on right side.

Branches of anterior crural:		
to pectineus	* + 21	Left at 48.
to sartorius, upper	+ 34	„ 52.
„ lower	+ 20	„ 53.
to rectus	+ 18	„ 52.
to vastus internus and crureus	+ 13	„ 54.
to vastus externus and crureus	+ 14	„ 54.
Nerve to tensor vaginae femoris	+ 7	„ 53.

Obturator:			
to gracilis	+ 13	Left at 57.	Muscle obviously wasted.
to adductor longus	+ 22	„ 54.	
to obturator externus	+ 27	„ 54.	
to adductor magnus	+ 19	„ 55.	

External Popliteal:		
to tibialis anticus	+ 32	Left at 55.
to extensor long. digitorum	+ 30	„ 54.
to extensor prop. pollicis	+ 28	„ 54.
to extensor brevis digitorum	+ 22	„ 56.
to peroneus longus	+ 34	„ 54.
to peroneus brevis	+ 33	„ 55.

Internal Popliteal:		
to external head of gastrocnemius	+ 18	Left at 54.

* The sign + denotes in this and the following experiments "Contraction obtained at."

to internal head of gastrocnemius.	Muscle much wasted.	
α branch	+ 9	Left at 54.
β branch	+ 7	,, 54.
to plantaris (much wasted)	+ 9	,, 57.
to soleus (wasted)	+ 7	,, 54.
to tibialis posticus	+ 25	,, 55.
to flexor longus hallucis	+ 26	,, 57.
to flexor perforans	+ 25	,, 56.

Internal Plantar.

Abductor hallucis and flexor brevis digitorum reply to strong stimulation of the trunk, i.e. current distinctly perceptible by the tongue.

External Plantar.

Adductor hallucis and accessorius reply to strong excitation of the trunk, i.e. current distinctly perceptible by the tongue. Adductor hallucis replies better than accessorius. No comparison made with left side.

3, vii. Male. The 6th, 8th, 9th and 10th roots of the right side anterior and posterior cut through proximal to the root-ganglia. Same evening, is very active in cage, moving rapidly but a little clumsily in coming *down* to the door. Picks up pieces of sugar with left, but not with right foot when hands are detained.

15, vii. No detected impairment of movement. Tail is turned to left. Right knee-jerk brisker than left.

26, viii. Knee-jerk brisker right than left.

Some wasting of inner hamstring and calf of right side.

Can grasp well with right foot.

Tail is kept turned to left strongly.

Anus normal in appearence.

Anterior crural, and obturator.

Muscular branches severally tried right and left, and no difference detected.

Nerve of hamstrings (sciatic branch):

to biceps, upper branch	+ at 31	Left at 50.
lower branch	+ at 33	,, 50.
to semitendinosus upper branch	+ at 28	,, 51.
lower branch	+ at 27	,, 50·5.
to semimembranosus	+ at 16	,, 51.
to adductor magnus	+ at 23	,, 51.

Internal popliteal trunk.

Nerve to internal gastrocnemius	+ at 20	Left at 52.
,, external ,,	+ 28	,, 52.
,, ,, ,,	+ 28	,, 52.

Nerve to soleus	+ 19	Left at 51.
„ plantaris	+ 22	„ 53.
„ popliteus	+ 38	„ 50.
„ flexor longus digitorum	+ 38	„ 52.
„ flexor longus pollicis	+ 42	„ 55.
„ „ „ „	+ 43	„ 53.
„ „ „ „	+ 43	„ 55.
„ tibialis posticus	+ 43	„ 55.

Internal Plantar.

Branch to abductor hallucis	+ at 39	Left at 59.
„ flexor brevis digitorum	+ at 39	„ 57.
„ flexor brevis hallucis	+ at 30	„ 58.
Two lumbricales (judged by exciting nerve-trunk after cutting the above branches, and obtaining slight flexion of 2nd and 3rd digits)	+ at 26	„ 58.

External Plantar.

Branch to abductor minimi digiti	+ at 35	Left at 53.
„ accessorius	+ at 35	„ 55.
„ flexor brevis minimi digiti	+ at 24	„ 60.
„ adductor hallucis and interrossei of 2 or 3 digits	+ at 22	„ 55.
„ lumbricales and interrossei of last two digits	+ at 18	„ 53.

External Popliteal.

Branch to tibialis anticus	+ at 30	Left at 46.
„ „ „	+ at 29	„ 47.
„ extensor longus digitorum	+ at 30	„ 47.
„ extensor proprius hallucis	+ at 29	„ 47.
„ extensor brevis digitorum	+ at 34	„ 48.
„ peroneus longus	+ 23	„ 50.
„ peroneus brevis	+ 29	„ 47.

nerve to obturator internus,	cont. good at 25	not compared with left
„ quadratus femoris,	cont. good at 25	

„ sphincter ani and levator ani together, some contraction to be obtained, but not so good as on left side, on excitation of pudic.

May 6, 1890. Male. On the right side the 6th, 7th, 9th and 10th roots cut through proximal to the root-ganglia.

May 7. Obvious clumsiness with right leg, difficult to say in what the defect consists; can grasp with right foot, but is reluctant to climb the cage. Prolonged observation detects performance at one time or another of all primary movements at all the joints, but flexion of the ankle and extension of digits are certainly imperfect. "Interosseal" flexion of the digits was noted and also once full flexion of the hallux (i.e. long flexor). No abnormal appearance of anus. Tail is kept turned to the left. Knee-jerk much brisker right than left. Squats, and rises from squatting posture without obvious difficulty.

May 28. No obvious clumsiness in movement. Peroneal flexion seems defective as tested by observer holding foot with sole inverted.

June 13. Anus normal in appearance. Knee-jerk brisker right than left. Calf muscles and hamstrings wasted on right side.

Muscular Branches of *anterior crural* and *obturator nerves* of right side reply at least as well as similar of left side.

Branches of Nerve-trunk to hamstrings.

to biceps, upper branch	+ 5	Left at 65.
" lower branch	+ 26	" 64.
to semitendinosus, upper branch	+ 23	" 64.
" lower branch	+ 28	" 64.
to semimembranosus	+ 30	" 65.
to adductor magnus	+ 33	" 63.

biceps is obviously wasted, especially at upper part.

Internal popliteal trunk.

Nerve to internal gastrocnemius	+ at 47	Left at 58.
" external "	+ at 34	" 56.
" " "	+ at 35	" 56.
" plantaris	+ at 14	" 57.
" soleus	+ at 9	" 58.
" tibialis posticus	+ at 22	" 56.
" " " and flexor longus hallucis	+ at 24	" 58.
" flexor longus hallucis	+ at 29	" 54.
" " " "	+ at 29	not found.
" flexor longus digitorum	+ at 23	Left at 56.
" popliteus	+ at 36	" 50.

Internal Plantar, branches of:—

to abductor hallucis	+ at 9.
to flexor brevis digitorum	+ at 8.
" " hallucis	+ at 10.
to two lumbricales (judged of by flexion of 2nd and 3rd digits on excitation of nerve-trunk after cutting the above branches).	+ 9

Left internal plantar gave contraction of all these at 40.

External Plantar, branches of:—

to abductor quinti	+ 9	Left ext. plant. gave contraction of these at 43.
to accessorius	+ 18	
to flexor brevis quinti	+ 10	
to adductor hallucis interossei and lumbricales	+ 8	Left at 38.

(At this part of the experiment both feet had become very cold.)

External Popliteal, branches of:—

to tibialis anticus	+ at 25	Left at 53.
,, ,,	+ at 26	
to extensor longus digitorum	+ 26	,, 55.
,, proprius hallucis	+ 22	,, 52.
,, brevis digitorum	+ 26	,, 56.
to peroneus longus	+ 29	,, 54.
to peroneus brevis	+ at 8	,, 52.
nerve to obturator internus	+ 32	,, 44.
,, quadratus femoris	+ 30	,, 44.

,, levator ani and sphincter taken together in pudic trunk. Reply good—not compared with left side.

The nerve to the left peroneus brevis when examined in osmic preparations in transverse section revealed largish fibres, and quite small fibres, a considerable amount of sclerosis was obvious, in fact it looked as though much more than half the nerve-fibres must have disappeared from the nerve. Among those remaining there was no trace of degeneration.

Feb. 1, 1891. Male. On right side the 7th, 8th, 10th, 11th, and 12th roots divided proximal to the root-ganglia. That evening obvious paresis of the leg. The leg was twice obviously at fault in getting across floor of cage; the clumsiness seems to lie at ankle joint. Ankle is kept in a somewhat flexed position; in springing up to bench from floor of cage the spring was made chiefly with the left limb. Foot can grasp. Root of tail deviates to left, and the tail itself is curved with concavity to left. No abnormality in anus. Knee-jerk decidedly brisker right than left.

Feb. 7. Far less clumsy. Very active.

Feb. 28. No obvious defect in movements in cage.

March 15. Right calf obviously shrunken, also wasting of outer hamstring; ? of inner also. Knee-jerk brisker right than left. Tail is directed and curved to left side.

Branches of nerve-trunk to hamstrings:

to semitendinosus	+ 20	Left side at 57.
,, biceps, upper branch	+ 18	,, ,, 58.
,, ,, lower branch	+ 8	,, ,, 59.
,, semimembranosus	+ 22	,, ,, 58.

Biceps is wasted, to inspection, but not especially at upper part.

Internal politeal trunk:

nerve to external gastrocnemius	+ 8	Left side at 60.
,, ,, ,, ,,	+ 6	,, ,, 60.
,, ,, internal gastrocnemius	+ 6	,, ,, 60.
,, ,, plantaris	+28	,, ,, 58.
,, ,, soleus	+11	,, ,, 59.
,, ,, flexor long. hallucis	+26	,, ,, 56.
,, ,, ,, ,, digitorum	+24	,, ,, 59.
,, ,, tibialis posticus	+29	,, ,, 57.
,, ,, popliteus	+20	,, ,, 58.

external saphenus n. half way down the calf gives adduction of hallux and flexion of all digits at 26, left side at 60.

internal plantar nerve gives flexion of hallux and all digits at 38, left at 63.

external plantar nerve gives adduction of hallux and all digits at 35, left at 59.

External popliteal trunk:

nerve to tibialis anticus	+38	Left side at 51.
,, ,, ,, ,,	+40	,, ,, 51.
,, ,, extensor proprius hallucis	+42	,, ,, 53.
,, ,, ,, longus digitorum	+41	,, ,, 54.
,, ,, ,, brevis digitorum	+38	,, ,, 54.
,, ,, peroneus longus	+43	,, ,, 54.
,, ,, peroneus brevis	+37	,, ,, 53.

The Knee-jerk.

The motor nerve concerned in the knee-jerk is well known to be the anterior crural, the muscle concerned to be the quadriceps extensor cruris. Not the whole of the quadriceps extensor or of the branches to it from the anterior crural trunk are, as I find, necessary for the "jerk." The muscles chiefly concerned in it are the vastus internus and a part of the crureus. The branches of the anterior crural nerve to those two muscles contain therefore the motor fibres involved. If the branch given by the anterior crural nerve to the vastus internus and adjoining part of the crureus be cut through, the knee-jerk disappears or almost disappears at once, although the nerves to the rectus femoris (both parts) vastus externus, the subcrureus and a part of the crureus, all remain intact. If on the other hand all the branches given by the anterior crural nerve to the rectus femoris, vastus externus, and a part of crureus are divided the "knee-jerk" remains brisk so long as the branch to the vastus internus and crureus be left intact.

Schultz and Fürbringer[1] were the first to shew that the cutting through of the lumbar roots abolishes the knee-jerk just as does section of the anterior crural trunk itself. In 1878 Tschiriew[2] stated that in the rabbit destruction of the cord at the level of the 6th lumbar nerve abolishes the knee-jerk; Prévost[3] in 1881 shewed that section of the posterior root of that nerve in the rabbit abolishes the "jerk." This observation, which has never been impugned, I have had frequent opportunity to confirm for myself; but I have found that section of the sixth root does not in every rabbit abolish the jerk and occasionally section of the 5th root alone suffices to do so.

In the cat in my experiments contemporaneous section of all the spinal nerve-roots (both anterior and posterior roots cut together) of the lumbo-sacral region, if the sixth be spared only makes the knee-jerk brisk, but section of the sixth root (anterior and posterior roots together) instantly abolishes the jerk.

Section of anterior roots adjacent to the 6th, even more than does section of the whole roots, anterior and posterior, increases the briskness of the jerk; it is the section of the efferent divisions of the spinal roots belonging to the great hamstring branch of the sciatic which plays the chief part in producing the briskness. When the jerk has been artificially exaggerated a slight persistence of it or its complete absence can be judged to a degree that is surprising to the experimenter. By using the exaggeration as a routine procedure one is enabled to state positively that section of the 6th lumbar posterior root (the 5th and other higher lumbar roots remaining intact) completely annuls the jerk. Section of only half the filaments composing the posterior root of the 6th is of itself sufficient to at once extinguish the jerk, at least it has been in each of five experiments; in two it was the upper set of the filaments that was divided, in three the lower set. In the same individual in which section of the posterior (dorsal) root of the 6th lumbar nerve abolishes the knee-jerk, section of the anterior root greatly diminishes the knee-jerk but does not abolish it. If the jerk be previously rendered exaggerated it is usually easy to detect that although very much reduced, indeed almost to extinction generally, the jerk is not absolutely abolished by the section. If then section of the ventral

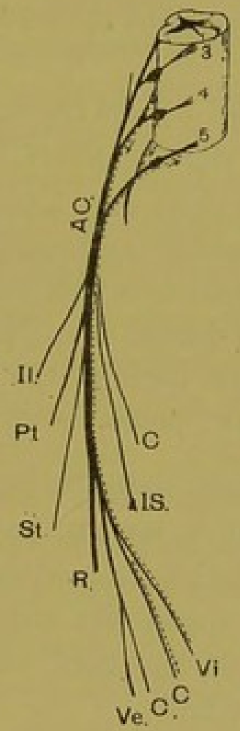
[1] *Ctbt. f. Med. Wiss.* p. 929.
[2] *Arch. f. Psych.* VIII.
[3] *Rev. Med. Suisse Romande, Mars*, 15.

root of the 5th be practised complete abolition of the jerk results forthwith.

In virtue of the very circumscript region of spinal outflow and inflow of the nerve-fibres which subserve it, the knee-jerk affords a somewhat facile test of the character of the plexal arrangement of the individual, i.e. of whether the arrangement belongs to the *prefixed* or *postfixed* class. In the cat the test was applied to twenty-five individuals with the result that in fourteen the jerk was abolished by section of the 6th lumbar root alone but in one it was not; in three it was almost extinguished by section of the 5th lumbar root alone, and in seven section of the 5th root did not obviously affect it. Of course it is possible that it would have been abolished by section of the 6th lumbar root alone in each of the ten cases in which section of the 5th did not abolish it. In three cases in which section of the 5th lumbar was chosen that root was selected because the intrinsic muscles of the foot had been previously suspected in the particular individual not to receive fibres from the 9th subthoracic but only from the 8th. In some individuals therefore the root on which the jerk chiefly depends is the 6th lumbar, in others the 5th lumbar.

In Macacus rhesus experiment revealed no instance in which section of the 5th root (whole root, anterior and posterior) failed to abolish the jerk. Section of the 5th lumbar root abolishes the "jerk" at once; on the other hand section of the adjacent roots may be practised contemporaneously on as many as seven or eight, without producing any effect on the jerk except to render it more brisk.

Section of the posterior root of the 5th lumbar spinal nerve abolishes the jerk at once, as also does section of even a half of it, (three experiments). Section of the anterior root of the 5th nerve I supposed after as many as eight experiments to completely abolish the jerk; it was only after repeating the experiment with previous section of the ventral roots of the 6th, 7th, 8th and 9th roots and vagal stimulation in order to exaggerate the "jerk" to the utmost that I was able to satisfy myself that the jerk in Macacus is not absolutely abolished by section of the efferent root of the 5th lumbar, but only very much diminished; a remnant of the jerk persists so long as the efferent root of the 4th lumbar remains intact. It may be urged that as regards the destructive effect on the "jerk" of dividing one half only of the filaments of the 5th posterior root the operation necessarily involves damage to the other half in the separation of the two sets of filaments. Some reply to this objection is offered by the following observation. On one occasion the cutaneous area of distribution of the 5th root was delimited before and after section of the half of the root, and was found to be hardly diminished at all by the section; on several occasions the cutaneous area of distribution of the area of the 6th root was delimited before and after section of half the posterior root and found to be hardly diminished at all by section of half its filaments. Therefore in these instances as judged by cutaneous reactions section of half a posterior root did not detectably damage the functions of the remaining half of the root. It became clear therefore that in macacus the efferent roots essential for the "jerk" are the 4th and 5th lumbar, the afferent root essential is the 5th lumbar.



I have referred to the fact that section of the anterior (ventral) roots of the spinal nerves below the ones on which the "jerk" depends renders the "jerk" more brisk than it is normally. Section of the posterior roots (dorsal) has a similar effect. This fact I did not notice until a great part of the above observations had already been made; its explanation appears to lie in the abolition of the tone of the hamstring muscles by section of the afferent roots belonging to them. This marked effect on the "jerk" of section of the afferent roots of the hamstring nerves and the lasting character of it is exemplified by the following.

Macacus rhesus ♀.

Dec. 9. 1890. Section of 6, 8, 9 sub-thoracic (dorsal) roots R.

Dec. 10. Knee-jerk brisker on right side than left.

Feb. 28, 1891. Knee-jerk brisker on right side than left.

Macacus rhesus ♀.

June 8. Section of the dorsal divisions of the 6, 7, and 9th left sub-thoracic nerves.

June 8. Knee-jerk brisker on left side than right.

Aug. 26. Knee-jerk brisker on left side than right.

Macacus rhesus ♂.

Dec. 14, 1890. Section of the dorsal roots of the 7th and 8th right sub-thoracic nerves.

Dec. 14. Knee-jerk brisker right than left.

March 5. Knee-jerk brisker right than left.

Macacus rhesus ♀.

Oct. 3. Section of the dorsal root of the 8th right sub-thoracic nerve.

Oct. 3. Knee-jerk brisker right than left.

Dec. 9. Knee-jerk brisker right than left.

Immediate and lasting results confirmative of the above were noted in other experiments on Macacus in which both anterior and posterior roots were cut together, cf. examples quoted above, pp. 660—666.

Section of the sciatic trunk itself at the upper part of the thigh also increases the jerk as Tschiriew[1] pointed out.

I have several times noticed that the lumbo-sacral region of the cord of rhesus may be divided by a longitudinal section carried along the middle line into right and left halves without impairment of the knee-jerk of either leg. I have made the slit from the origin of the 2nd lumbar rootlets to the end of the cord without obviously diminishing the knee-jerk either right or left.

It may be noted in passing that in rhesus after transverse section of the cord at the level of the 9th thoracic the knee-jerk disappears, in my experience, in about 10 minutes' time: it disappears to return gradually, first becoming detectable in about three' weeks time; from its reappearance onward the jerk gradually increases until in a couple of months it is exaggerated and remains so. After a complete transverse section of the cord at the level of the 1st lumbar root with partial section at the 3rd lumbar the jerk disappeared, but not to reappear, at any rate not for six months through which observation was continued.

The abolition of the "jerk" produced by the cutting of the posterior

[1] *Arch. f. Psych., loc. cit.*

root of the 5th lumbar in macacus or of the 6th in cat and rabbit is immediate. The "jerk" when tested 12 seconds after section of the root is gone. After complete transverse section of the cord at the 1st lumbar the "knee-jerk" becomes, in the cat, almost at once, i.e. in a few minutes, exaggerated, and this forms a favorable circumstance for testing its presence or its absence. In macacus the section of the spinal cord has not that re-enforcing effect, and observation on the "jerk" becomes difficult from failure of the phenomenon under the general depression induced by the operative procedure and prolonged action of the anæsthetic. So serious is the difficulty with Macacus that I at one time nearly abandoned observations on immediate effects upon the "jerk." For the sake of others who may find the same difficulty I may say that one finally met it successfully by employment of certain influences which tend to immediately exaggerate the "jerk"; one method at command lies in section of the anterior roots of the 6th, 7th, and 8th sub-thoracic spinal nerves (motors to hamstrings) or of the posterior roots of the same nerves; another lies in strong excitation of the distal end of either of the vagus nerves which as a result of the minimal blood pressure soon causes a brisk "jerk" even if the "jerk" be absent when the excitation is commenced (extensor spasm of a tonic nature may eventually supervene); a third method is induction of dyspnœa, which as lately shewn by Hughlings Jackson and R. Russell usually exaggerates[1] the "jerk" at a certain stage before finally depressing it. It may be added that I find both the vagal and dyspnœic increase can be produced after the cord has been previously severed in the thoracic region, so are, at least in part, spinal.

With regard to the effect of anæsthetics on the "jerk," a better proof of the action of chloroform being rapid and direct on the nervous mechanisms of the cord itself could hardly be found than in the speedy abolition of the "jerk" by chloroform inhalation when the cord has been previously divided in the thoracic region. In a Macacque in which the cord had been transversely divided at the 9th thoracic root-level five months previously, chloroform abolished the "jerk" within a few seconds after abolishing the eyelid reflex, and as quickly as in a normal Macacus chloroformed at the same time. In the cat even when the "jerk" is exaggerated, the cord having been divided a short time previously (thirty minutes), on pushing the depth of anæsthesia the "knee-jerk" fails as rapidly, it has seemed to me, as before the cord has been divided. One difference has however appeared to exist in the effect of the anæsthetic on the "jerk" after the

[1] J. Hughlings Jackson. *Brit. Med. Journal*, Feb. 13, 1892.

lower cord is isolated by section in the thoracic region namely, that on discontinuance of the inhalation the "jerk" is tardier in its reappearance when the lower region of the cord has been isolated than when its connection with the upper cord and brain remain intact.

SECTION III.

MOTOR ROOTS TO MUSCLES OTHER THAN THOSE OF THE LIMB.

Of the Anus.

When all the nerve roots of the sacral region have been divided both right and left the anus still remains closed in the cat and macaque; but it is less retracted than in the normal condition, indeed it may protrude somewhat. On being opened by the passage of for instance a surgical sound it does not grip the instrument and remains patent after the withdrawal of the sound. If then certain of the anterior nerve roots be stimulated smart closure of the orifice immediately follows.

The nerve roots which give this closure are in the cat, the 8th and 9th sub-thoracic, more rarely in my experiments the 7th. In macacus rhesus the nerve roots which close the anus[1] have been in sixteen experiments the 7th, 8th, 9th. I met with no instance in which the 10th root gave closure of the anus. The action was most easily and powerfully induced by the 8th root; often the action was very feebly represented in the 7th root, occasionally very feebly in the 9th root.

In both of two experiments on the bonnet monkey, the anus was very forcibly contracted on excitation of the 7th root, quite feebly on excitation of the 9th root; this result being an instance of the high type which in my few experiments seemed to prevail in the bonnet monkey.

Two points of interest may be mentioned in regard to the innervation of the sphincter ani. The anus does not become patulous, that is to say it does not remain patent for a time after being thrown open, so long as any one of the motor roots supplying it remains uncut; further when of the six roots supplying it, all three of one side were divided, no asymmetry of the anal orifice when the sphincter was at rest or sometimes when in action was detected. Secondly, excitation of for instance the right hand roots supplying the sphincter appeared at first sight, if strong, to cause a contraction of the entire circumference of the

[1] Cf. Sherrington. *Brit. Med. Journ.* May 9, 1891.

orifice; sometimes it was hardly obvious even that the right hand half of the sphincter contracted more vigorously than the left, although on minute examination especially under minimal excitation that did always seem to be actually the case. An incision carried through the sphincter along the median line of the body limits the contraction to the half of it on the same side of the body as is the nerve root subjected to excitation. On one occasion, in the rabbit, the 8th root gave with minimal currents a contraction of the anus almost limited to one side. On one occasion in Rhesus, division of the 8th and 7th roots of the left side made the anal orifice obviously asymmetrical.

This overlap of the distribution of motor fibres of the right and left halves of the body is comparable to the crossing of the median line by the pilo-motor fibres to the scalp and tail[1], or to the mutual interference of action of the inhibitory fibres of the right and left vagus nerves in their influence upon the heart[2].

But the relationship of action between the portions of the sphincter situate on either side the median line is very close. Constriction and protrusion of the anus, either both movements together or one apart, may be very readily elicited by excitation of the proximal piece of the 9th or of the 8th sub-thoracic posterior (afferent) root after section of that root in the spinal canal. The anal closure thus reflexly evoked rarely betrays the unilaterality of its source of origin.

Constriction and protrusion of the anus can also be induced by excitation of the cerebral hemisphere. Movement of the anus, generally constriction with or without protrusion, can be elicited from the whole of the somewhat extended area of cortex shaded in Figs. 4, 5, Pl. XX. Indeed it may ensue on excitation quite outside that area if the excitation be pushed to the production of epileptoid convulsions; its place in the sequence of the Jacksonian "march" will then be late, but is early if the excitation is similarly pushed within the area indicated in the figure. By weak stimulation in the small area marked A in the figure movement of the anus can be obtained unaccompanied by movement of other parts, or by constriction of the vaginal orifice only. As the electrodes are gradually shifted from that focal area backwards movements of the anus, vagina, and pedal digits are evoked together or in various sequences; when the electrodes are set further forward than the focal region (A), movements of the anus, vagina, and tail result, the tail often leading in the sequence undergoing adduction toward the side opposite that on

[1] Langley and Sherrington. This *Journal*, Vol. XII. p. 278.

[2] Gamgee and Priestley. This *Journal*, Vol. I. p. 39; Tarchanoff, *Arch. de Phys.* 1875.

which the cortex is excited. The cortical focus for movement of the anus lies therefore in Macacus medial to Ferrier's[1] "tail centre," and near the "glutœus" centre of Schäfer and Horsley on the medial aspect of the hemisphere[2].

Now anal movement evoked from the cortex is, although not strictly unilateral, more marked on the crossed side than on the same side of the body. If the left cortical area be excited with minimal currents the right side of the anus moves obviously more than does the left; when the pitch of excitation is gradually increased it becomes less easy and soon difficult or impossible to detect a preponderance of the action of either side.

A light lever lodged in the anal orifice greatly assists the detection of inequality of the bilateral action of the anus by shewing deflection to either side from a neutral position of rest in the median plane.

The close association between the action of the two sides is well displayed by experiments of which the following will serve as example.

Macacus rhesus, ♀. A. C. E. mixture. Lower lumbo-sacral roots of the right side exposed in the spinal canal. Upper part of left "motor" cortex uncovered. Excitation of a point (α) on mesial face of hemisphere 3 mm. below top of marginal gyrus, and opposite posterior end of sulcus x, evokes closure of anus without other movement or as opening movement of a sequence which runs 1. closure of anus, 2. closure of vagina, 3. extension of the pedal digits with adduction and flexion of hallux. Another point (β) is found about 2 mm. behind top of sulcus centralis which under weak excitation gives flexion and adduction of the hallux without any movement of anus.

11.5. A.M. Secondary coil at 14 cent. Electrodes applied at point (α) give a closing movement of the anus markedly preponderant on the right side of the median line.

11.6. Electrodes applied at point (β) give adduction and flexion of hallux of right side without any movement of left hallux.

Then the 10th, 9th, 8th, and 7th sub-thoracic roots on the right side are cut through.

11.8. Secondary coil at 14 c. Electrodes applied at (α) evoke no movement in anus, and (β) no movement in either hallux.

Secondary coil at 13 c. Electrodes applied at (α) evoke movement in anus chiefly on left side of median line. Applied at (β) no movement in either hallux.

Secondary coil at 12 c. Movement at anus evoked from (α) appears to

[1] *Proc. Roy. Soc.*, 1875.

[2] *Phil. Trans.* 1888, B. p. 11; Schäfer, *Ludwig's Festgabe*, p. 269.

involve whole circumference of orifice, but preponderates on left side. No movement of either hallux elicited from (β).

Secondary coil at 11 c. At (α) excitation gives strong closure of the anus not obviously asymmetrical in character. At (β) excitation gives no movement of either hallux.

Secondary at 10 c. Same as above.

Secondary at 9.5 c. (α) as before. Excitation at (β) gives adduction of *left* hallux, but no movement of right hallux.

Thus the increment of exciting current requisite to evoke by cortical stimulation contraction not only on the crossed side of the anal sphincter but also on the side in the same half of the body as the hemisphere excited, is less than the increment required to evoke movement of the "uncrossed" hallux as well as of the "crossed."

Of the vagina.

Closure of the entrance to the vagina results in Rhesus on excitation of the 8th and 9th sub-thoracic roots, (2nd and 3rd sacral). Three times in sixteen experiments excitation of the 7th root gave a dubious contraction. In the cat excitation of the 8th and 9th sub-thoracic roots, causes strong constriction of the orifice of the vagina. The closure is sharp, and the contraction which brings it about not limited strictly to the orifice but to be felt by the finger extending for some distance up from the orifice. Usually the 9th causes a rather more powerful contraction than the 8th. As in the case of the anus, moderately strong excitation of a root on the right or left side appears to throw into action both sides of the sphincter. The contraction is in a sense bilateral. An incision through the sphincter in the median line prevents the half on the side opposite to that to which the nerve root stimulated belongs from participating in the action.

Just as for the anus so also for the vaginal orifice an intimate relationship exists between the movements of the portions situated on the opposite sides of the median line. And just as anal movements are elicitable by excitation of the cortex cerebri, so also are movements of the vaginal orifice, each hemisphere being preponderantly connected with the musculature of the opposite half of the sphincter. The cortical area from which movements of the vagina are elicitable is not so extended as that productive of anal movements, at least not in the individuals examined by me which it is to be remembered were not sexually mature. The focus of the area for vaginal movement was found a little (2 mm.) in front of the focus for anal movements. In the adult cat and dog this focal area is easy of demonstration and lies in the posterior limb of the sigmoid gyrus just mesial to the front end of the ansate fissure of Langley[1], (cf. fig. 6, Pl. XX.).

Bechterew and Mislawski[2] in a recent paper state that the rhythmic contractions of the vaginal cavity of the Rabbit and Dog can be augmented or diminished by stimulation of various parts of the brain, among others of the posterior limb of the sigmoid gyrus in the latter. My own observations relate only to the sphincter muscle of the orifice and that does not under ordinary circumstances display tonus obviously rhythmic in character.

Of the Urinary Bladder.

Our first accurate knowledge of the relation of the motor nerves of the bladder to spinal nerve roots is due to Budge[3]. From experiments on dogs he concluded that two sets of nerves exist for the bladder, the one set contained in the anterior roots of the 1st, 2nd, and 3rd sacral nerves, the other set in the hypogastric plexus; the latter set he believed sensory, the former set motor. "Im plexus hypogastricus liegen nur sensible Fasern und keine motorischen[4]." Sokownin writing five years later recorded that excitation of the spinal cord in the neck produces contraction of the bladder even after the cord has been cut across at the level of the 7th lumbar nerve[5]. H. Nussbaum[6] found in the cat that (1) motor fibres to the bladder pass out from the cord in the 2nd and 3rd sacral roots, and also to a slight extent in the 1st sacral root, and (2) that some motor fibres to the bladder leave the cord just below the level of the 3rd lumbar and enter the sympathetic chain. Langley speaking recently of the innervation of the pelvic viscera in the rabbit says "The bladder likewise has a nervous supply in general similar to that of the descending colon[7]." Of the descending colon he says: "There is a set of motor fibres in the 2nd, 3rd and 4th sacral nerves perhaps also in the 1st, but chiefly in the 3rd and 4th. There are also efferent fibres to the colon in the lumbar sympathetic chain, stimulation of it from about the 2nd to the 6th ganglia of the

1 This *Journal*, Vol. IV. p. 248.

2 *Archiv f. Physiol.*, March 17, 1892.

3 *Zeitschr. f. ration. Med.* 1864, XXI. p. 1 and 174.

4 *Pflüger's Archiv*, 1872, VI. p. 306.

5 Russian, reported in Hoffman and Schwalbe's Jahrsbericht, VI. iii. 87 (1877).

6 Russian, reported in Hoffman and Schwalbe, VIII. ii. 64, (1879).

7 J. N. Langley. *Proceedings of Physiological Society*, Dec. 13, 1890. This *Journal*, Vol. XII. p. xxiii.

sympathetic chain causes usually a brief contraction of the descending colon."

Still more recently the motor nerves of the bladder have been experimentally investigated by Nawrocki and Skabitschewsky[1]. Their experiments were made upon the cat as were Nussbaum's and my own, and they found that the motor nerves of the bladder consist of two sets. An upper set passes from the spinal cord by the anterior roots of the 4th and 5th lumbar nerves, a lower set by the anterior roots of the 2nd and 3rd sacral nerves, and thence into the plexus hypogastricus.

All of the above-mentioned observers determined the presence or absence of contraction of the bladder by simple inspection of the organ when exposed to view.

In 1882 Mosso and Pellacani registered the movements of the bladder graphically and shewed that the bladder like the spleen (Roy) is continually undergoing rhythmic contraction. This fact is indeed most salient in any experimental investigation of the organ by the graphic method (Figs. 4, 5 and 7; Plate XXII.). In attempting in Macacus to ascertain which nerve-roots contain efferent fibres to the viscus, the difficulty of distinguishing by simple inspection the effect of the nerve-root upon an organ constantly pulsating under spontaneous contractions seems to demand the use of graphic records for the purpose.

Therefore in all the observations on which the following description is based contraction of the bladder was recorded by a graphic method. The registration was effected without opening the abdominal cavity at all. A glass cannula introduced through the membranous urethra well into the cavity of the bladder connected the urine inside the organ with a water-filled system ending in a wide water manometer. A float in the latter conveyed its own movements depending on alterations in the surface-level of the water to the long arm of a light and counterprised lever. The width of the manometer tube was made great enough to avoid complicating the record by subjecting the bladder to any but insignificant changes of pressure; the records may be considered therefore rather as volumetric than manometric. The water in the recording system was kept approximately at the temperature of the blood. In some of my experiments the viscus was relieved from the variations in intra-abdominal pressure that accompany the respiratory movements by the laying that cavity freely open along the linea alba;

[1] *Pflüger's Archiv*, Vol. 49, p. 141, 1891. A Note of my own observations in Macacus was published May 9, 1891, in the *Brit. Med. Journal*.

but the variations in intra-abdominal pressure were found to be very small, and it is easy to record them synchronously on the same cylinder as receives the bladder trace, if a very thin walled and flexible bag is introduced into the abdominal cavity, filled with water and connected with a water manometer, the level of the water in the manometer being recorded by a float, without magnification. The registers of two experiments performed in this way showed the variations in intra-abdominal pressure during the deep anæsthesia induced to be so extremely slight, not more than two millimetres of mercury, that they may be disregarded as sources of confusion in the interpretation of such extensive alterations in the volume of the urinary bladder as resulted from excitation of certain anterior roots.

The number of experiments made to determine the position of the efferent outflow to the bladder was sixteen, seven in the cat, nine in macacus. As the results have not been quite constant they are given in tabulated form.

On the Cat.

	Exp. I.	Exp. II.	Exp. III.	Exp. IV.	Exp. V.	Exp. VI.	Exp. VII.
13 thoracic	0	0	0	0	0	0	0
1st lumbar	0	0	0	0	0	0	0
2nd ,,	0	0	0	0	slight	0	slight
3rd ,,	slight	slight	moderate	slight	strong	slight	strong
4th ,,	strong	strong	strong	strong	strong	strong	strong
5th ,,	strong	strong	strong	strong	?	moderate	slight
6th ,,	0	0	0	0	0	0	0
7th ,,	0	0	0	0	0	0	0
1st sacral	slight	fairly strong	strong	slight	strong	slight	strong
2nd ,,	very strong	very strong	very strong	very strong	very strong	very strong	very strong
3rd ,,	strong	fairly strong	moderate	strong	slight	strong	slight
4th ,,	0	0	0	0	0		

On Macacus rhesus and one Bonnet monkey.

	Exp. I.	Exp. II.	Exp. III.	Exp. IV.	Exp. V.	Exp. VI.	Exp. VII.	Exp. VIII.	Exp. IX.
12 thoracic	0	0	0	0	0	0	0	0	0
1st lumbar	slight	0	0	0	0	0	0	0	0
2nd ,,	moderate	slight *	slight	slight	slight	slight	?	slight	moderate
3rd ,,	moderate	moderate	moderate	moderate	moderate	moderate	moderate	moderate	moderate
4th ,,	slight	moderate	moderate	moderate	moderate	moderate	moderate	slight	slight
5th ,,	0	?	0	0*	0	0	slight	0	0
6th ,,	0	0	0	0*	0	0	0	0	0
7th ,,	0	0	0	0	0	0	0	0	0
1st sacral	strong	slight	slight	moderate	slight	slight	slight	moderate	strong
2nd ,,	strong*	strong	strong	strong	strong	strong	strong	strong	strong
3rd ,,	0	strong	moderate	moderate	strong	strong*	strong	slight*	0
11 subthor.	0	0	0	0	0	0	?	0	0

* Fig. 2 (Exp. I.) * Fig. 3 (Exp. II.) * Fig. 6 (Exp. IV.) * Fig. 8 (Exp. VI.) * Fig. 9 (Exp. VIII.)

It will be seen therefore that in the cat the observations agree closely as regards the sacral outflow with the original observations of Budge, but that they confirm the more recent observations as to the existence of a motor outflow in the upper lumbar anterior roots.

In the seven experiments on the Cat motor fibres were present each time in the 1st, 2nd and 3rd sacral, and in the 3rd, 4th and 5th lumbar roots, on two occasions in the 2nd lumbar root also. The lowest two lumbar pairs were on no occasion found to contain motors to the bladder. In macacus in each of nine experiments the 1st and 2nd sacral and the 3rd and 4th lumbar roots contained efferents to the bladder, in eight of the experiments there were efferents also in the 2nd lumbar root, in seven in the 3rd sacral root, in one probably in the 5th lumbar root. With that one perhaps doubtful exception the lowest three lumbar roots gave no evidence of efferents to the bladder.

These are therefore the lower and upper sets of efferent fibres to the bladder from the spinal cord. Of these the lower set causes the more powerful contraction in the viscus. This can be seen from the tracings in Figs. 2 and 3, Plate XXII. The contraction produced by the 2nd sacral root is usually more powerful than that produced by any other root. The contraction produced by the sacral roots appears somewhat different in character to that produced by the lumbar roots; it is not only more powerful but follows more quickly on the excitation, and often appears not to be so long lasting as is the contraction caused through the upper lumbar roots (cf. tracings Figs. 2 and 6 with 3, Plate XXII.). These differences may perhaps all have their explanation in mere strength of contraction, and be less qualitative than merely quantitative in character. The slighter and less abrupt contractions given by the upper lumbar roots require some word in passing to relieve them from suspicion of being a simply mechanical result of respiratory action or of compression by the muscles of the abdominal wall also innervated by the upper lumbar ventral roots. Regarding the first point it suffices to say that they can be produced under curarisation or when the respiration has been stopped by pushing the administration of chloroform; regarding the second point the answer is that they persist when the lumbar nerves have been cut through from the interior of the abdomen outside the edge of the psoas muscle. An objection more difficult to meet is that they are nothing else than the spontaneous contractions of the bladder which recur from time to time; this latter suspicion gains weight from the fact that the time elapsing between the excitation of the lumbar root and the contraction of the bladder so evoked is often long and appears to be somewhat variable, and further from the fact that, at least in my experiments the phenomenon although the rule, sometimes lapses unaccountably, even in the course of an experiment in which it has been and later becomes again obtainable with great constancy.

In order to critically examine this objection I endeavoured first to bring the bladder into a condition of rest and of freedom from rhythmic contraction by performing transverse section of the cord in the lower dorsal region. Goltz[1] it is true, pointed out as long as eighteen years ago, that normal micturition may take place in a dog in which the lumbar region of the cord has been completely and permanently separated from the upper dorsal region by section. In his experiments, days or weeks were allowed after the performance of the section for restoration of the functions of the cord. But A. Mosso and Pellacani[2] found in experiments made on the same day as the operation on the cord was performed, that section, even incomplete, of the spinal cord in the lower dorsal region, that is to say section carried through only the posterior columns and the posterior part of the lateral columns, sufficed to annul all active contractions in the bladder even when stimulation was applied not only to the fore limbs but also to the hind limbs, i.e. pinching hind foot etc. "L'excitation des extrémités antérieures reste sans résultat; il en est de même des extrémités postérieures." I was somewhat surprised to find that in my experiments complete transverse section of the cord at the level of the 12th thoracic root did not in Macacus, or in the cat, arrest the movements of the bladder even temporarily. The effect of the section is to cause a strong contraction of the viscus, which after that contraction has passed off subsides again at once into a state of rhythmic activity not obviously different from what it exhibited previous to the section. The rhythmic activity is literally not interrupted for more than a couple of minutes, if indeed it can be said to be interrupted at all when the interruption is of the nature of a spasm and in no sense a relaxation or repose.

Section of the cord having thus failed in my hands to arrest the bladder contractions it remained to try combined section of all the anterior roots of the nerves supplying motor fibres to the organ. As motor fibres to the bladder had never been evidenced in the 6th and 7th lumbar roots and as those roots are large and accompanied by large

[1] *Pflüger's Archiv*, 1874, p. 478.
[2] *Arch. Italiennes de Biol.* 1882, p. 33.

veins and as I did not desire to add to the adverse conditions of a necessarily severe operation, I determined to leave those roots intact, but to cut all the other nerve roots lumbar and sacral in the spinal canal both on right and left sides and both in their dorsal and ventral divisions. This done I found the rhythmic activity of the organ still continue.

The tracing in Fig. 4, Plate XXII. illustrates the rhythmic activity of the bladder after section of all the above-mentioned roots. The form of the contractions can be clearly seen in spite of complication by somewhat irregular respiratory movements. It might be urged that irregularity of the respiratory movements here really largely produced, by cumulative action, the variations obvious in volume of the bladder; to escape such source of fallacy curare was then administered in the same experiment and twenty minutes later a further tracing (Fig. 5, Plate XXII.) taken with artificial respiration removed and with A. C. E. mixture pushed for the time to an extent sufficient to ensure absence of all extraneous muscular movement. It will be seen that the vesical rhythm persists in a practically unaltered manner in spite of these conditions. The inference to be drawn must be that the causation of the rhythmic contraction appertains to the peripheral ganglia connected with the motor nerves of the bladder or to the muscular tissue of the organ. To test this point the following experiments were employed. The bladder was connected as in the other experiments with the recording volumetric gauge, and the animal then killed by rapid blood-letting from the carotid; the bladder record was allowed to continue when death had occurred, and it was then seen that long after the heart had ceased to beat the contractions of the bladder went vigorously forward. The tracing in Fig. 1 was obtained 50 minutes after death. The irregularity of the curves was at first a little surprising, but is explicable as the result of the interference of some other contractions with the vesical, whether of adjacent viscera as seems most probable or of the abdominal wall itself (cp. Brown Sequard's observations on the *post mortem* contractions of muscle[1]) does not appear quite certain. This irregular character of the curves of bladder contraction disappeared on opening the abdomen and shielding by wire guards the bladder as it lay *in situ* from direct contact with adjacent viscera and from the anterior wall of the abdomen. The regular character of the curves then obtained is exemplified by the tracing Fig. 10, Plate XXII.

Similar contractions but not in such equable or long lasting series

[1] *Arch. de Physiologie norm. et path.* p. 675, 1889.

can be obtained by removing the viscus from the recently killed animal, placing it in normal saline solution at a temperature of 38° C. and connecting the interior of it with any volumetric recorder. For this purpose the bladder of the dog answers better than that of Macacus or of the cat. The temperature must be carefully adjusted; a pressure of 2—4 cm. of water for the monkey's bladder, of 4—8, for the dog's bladder constitutes a favourable condition, although it must be remembered that in employing such an adjuvant as pressure one is perhaps introducing a new factor in the shape of direct excitation by tension of the muscular fibres of the wall.

It seems therefore justifiable to suppose that here, just as Engelmann has shewn to be the case in the middle third of the ureter of the rabbit, and as Gaskell, Luchsinger, McWilliam and others have shewn of the heart of the frog, tortoise, &c., the rhythmic action of the monkey's bladder arises in its own muscular wall. Its 'beat' like the heart's is of intrinsic origin.

It is therefore not easy to reduce the spontaneous contractions of the bladder so that an even line is obtained on the graphic trace from which as from a zero level any small contractions caused by direct excitation of a certain number of efferent fibres will rise upward in an unmistakable manner. By pushing the chloroform anæsthesia to a severe depth after a heavy dose of morphia combined with atropin the spontaneous contractions are often greatly reduced and it was under these conditions that tracings like those seen in Figs. 2, 3, 6, 9, Plate XXII. were obtained. The tracings reveal unequivocal diminution in the bladder-capacity on excitation of the particular roots already enumerated in the tabular statement. The contraction of the bladder produced by excitation of the lumbar roots is considerably weaker than the contraction elicited by the sacral roots, and this difference appears to be more marked in macacus than in the cat.

The region of outflow of the motor fibres to the bladder is both in Macacus and cat a region of considerable longitudinal extent.. The region of lumbar outflow does not appear to be quite the same in the two types; in the monkey instead of extending as low as the 5th root it generally descends only to the 4th root; on the other hand in Macacus it extends upward to the 2nd lumbar root but in the cat I have not found it above the 3rd. In Rhesus the upper end of the whole outflow is at the 2nd lumbar root, the lower end at the 3rd sacral root. But a break in this outflow occurs about half-way down it; in none of nine experiments could I obtain any contraction of the bladder from excitation of the 6th and 7th lumbar roots and only in one of nine individuals from the 5th root (perhaps a doubtful exception). In the cat a similar break lies at the two lowest lumbar roots (again the 6th and 7th subthoracic.) If as one may suppose (*vide infra*) the position of the outflow of the efferents fairly indicates the position of the nucleus whence they come then we may suppose that a long nucleus for the bladder exists in the lumbo-sacral region, which has however a gap in its continuity, the gap corresponding to the cord segments between the 5th and 8th sub-thoracic. The outflow from the anterior roots above the gap is into the sympathetic system, from the anterior roots below the gap is direct by the sacral nerves. To a suggestion as to the wherefore of this gap I hope to return later.

A marked difference between the character of the contraction of the bladder produced by excitation of any of its motor spinal roots and the contraction similarly produced in the anal or vaginal orifices is the stricter unilaterality of the former (bladder) as compared with the latter. The most powerful motor root to the bladder, *e.g.* 2nd sacral, causing as it does most forcible contraction of the viscus does not give a contraction which obviously oversteps the median line of the viscus. This fact one first learnt when with Dr Joseph Griffiths in 1888 engaged in the laboratory in some experiments still unpublished. The opposite half of the bladder is merely passively affected nor does the wave of contraction obviously spread from the active half of the organ to the passive—a remarkable fact considering the unstriate nature of its muscular tissue. Under the contraction the shape of the viscus becomes asymmetrical and is curved over to one side in a manner too striking to be forgotten if once seen. I have up to the present looked in vain for unequivocal evidence of contraction of the bladder in reply to cortical excitation, either in monkey, cat or rabbit.

Of the Cremaster Muscle.

The cremaster muscle is in Rhesus thrown into contraction and the testicle is therefore, when descended, raised on excitation in the spinal canal of the second and third lumbar anterior roots. The contraction caused is sometimes more vigorous in the case of the 3rd than of the 2nd root, and never vice versa so far as I have seen (nine individuals). In one experiment excitation of the 2nd lumbar caused no contraction of the cremaster, but in that experiment excitation of the 4th lumbar gave good contraction of the cremaster, which it did not in any other experiment do. I have paid particular attention to the innervation of the cremaster because Ferrier and Yeo did not obtain contraction of it on stimulating the second lumbar root, a fact of some importance in translating their results to man[1]. In my own experiments contraction to the 2nd root happened constantly until the seventh experiment was reached. Once only out of the nine experiments did excitation of 2nd lumbar fail to elicit contraction of the cremaster.

Of the round ligament of the Uterus.

On excitation, inside the spinal canal, of the 3rd lumbar anterior root of Rhesus, the round ligament of the uterus is immediately thrown into contraction[2], the contraction lasting within limits as long as the tetanising current is maintained. Excitation of the 2nd lumbar root has the same effect; occasionally (twice in eleven observations) excitation of the 4th lumbar produced the contraction; in one of these two exceptional instances, the 2nd lumbar root did not produce the contraction which it had in every other instance done.

In the cat a similar contraction of the round ligament is produced by excitation in the spinal canal of the 3rd and 4th lumbar anterior roots. Outside the spinal canal the nerve-fibres causing the above effect on the round ligament can be found in the trunk of the genito-crural nerve and followed into the genital branch.

So quick and steady is the contraction produced that I could not believe it the contraction of muscle fibre of the nonstriate kind, and therefore examined microscopically the tissue of the round ligament of rhesus and found it to consist of striate muscle fibre of ordinary appearance. On searching the literature of the subject I find that the text-books with as far as I know but one exception describe the ligament as consisting of plain muscular fibre, and make no mention of striate fibre in it. Rainey, the teacher of Anatomy at St Thomas's Hospital, pointed out in 1845[3] that the human round ligament consists in great part of muscular tissue of the striate kind. Regarding its contraction, it is at the portion near the brim of the pelvis that this is best seen and seems to be more vigorous at any rate than it is near the uterus.

I have carefully looked to see whether any difference in the contraction of the ligament following the separate excitation of the two lumbar roots respectively is detectable, but I have failed to discover any except in some cases in the vigour of the contraction; the contraction pro-

1 Gowers, *Dis. of the Nerv. Syst.* Vol. I. p. 91.
2 Sherrington, *Brit. Med. Journ.* 1891.
3 *Philosoph. Transactions*, 1845.

duced by the 3rd lumbar root in Rhesus is often more vigorous than that produced by the 2nd root. Especial attention was paid to the locality of the contraction in the ligament; for each nerve the focus of contraction seems to be close outside the brim of the pelvis.

When the ligaments of both sides are thrown into contraction by simultaneous excitation of both 3rd lumbar roots or both genito crural nerves, a movement of the uterus is brought about. The movement is a tilting forward of the fundus with perhaps some depression of the whole organ. The movement of the uterus produced is however a feeble one, at least in my experiments it was so. My Macacques have it is true not been sexually mature.

A point of interest regarding the phenomenon may be noticed here. I first observed the contraction of the round ligament in the early spring (of 1890) in two monkeys. I had no more monkeys available at the time, but was anxious to observe the contraction further. I therefore turned to its study in the cat; five of the next six cats however obtained at that season were pregnant and in not one of the pregnant animals did one observe that any structure in the position of the round ligament contracted at all on excitation of the spinal roots, or of the genito-crural nerve, but I have since then repeated the experiments on numerous occasions and never failed to obtain the contraction in non-pregnant individuals. A pregnant Macacque I have never yet obtained.

Of the Vas deferens.

In the male Macacque, and the same is true for the cat, the vas deferens can be caused to contract by excitation in the spinal canal of certain of the lumbar anterior roots[1]. These roots are in Rhesus the 2nd and 3rd lumbar, in the cat the 3rd and 4th lumbar. The fibres giving this result can be found outside the spinal canal in the genito-crural nerve, and in the genital branch of that nerve. The contraction of the vas is quite different in character from the contraction produced in the round ligament by excitation of the nerve roots supplying that structure. An interval of time easily perceived without aid of graphic measurement elapses between the contraction of the vas and the commencement of the root-excitation. And the contraction is of a slow and peristaltic kind, and does not cease immediately on withdrawal of the stimulus.

[1] Sherrington, *Brit. Med. Journ.* May 9, 1891.

Of the Nervi erigentes.

In Rhesus an imperfect turgidity of the penis is produced by excitation of the anterior roots of the 8th and 9th sub-thoracic nerves. I believe the imperfect character of the erection obtained was due partly to the deep anæsthesia and partly to my specimens being too young to be sexually matured; I have for these reasons attempted the observation in two instances only. In the cat I find turgidity of the penis produced by excitation of the 8th and 9th sub-thoracic anterior roots, and in less degree through the 7th root. This agrees with the result recently obtained by Morat in the dog, where excitation of the 1st and 2nd sacral anterior roots produced erection of the penis. Morat[1] in his paper dwells on the fact that the nervi erigentes pass through the ventral (anterior) division of the root; Gaskell[2] had shown this four years previously in the case of the rabbit, in which animal he says the nervi erigentes pass through the anterior roots of the 2nd and 3rd sacral nerves. The rabbit often possesses only six lumbar vertebræ instead of the seven present in cat and dog.

Of the Hair on the buttock, thigh and tail.

The hairy coat of macacus in these regions is supplied by pilomotor fibres issuing from the cord in the anterior roots of the 1st, 2nd, and 3rd lumbar nerves and 12th dorsal. I have given details concerning the distribution in a conjoint paper with Mr Langley published in this *Journal*[3].

Section IV.

Relation of the limb to cell-groups in the spinal cord.

It is abundantly clear from the foregoing that the muscles of the limb which are supplied by the most posterior of the efferent nerve-fibres to the limb are the small muscles lying at the distal end of it. Is it possible from this fact to obtain a hint as to the position in the cord of the nerve cells which preside over that group of muscles? I have examined the cords of cat, macacque and man with regard to this point. A number of physiological facts make it probable that the nerve-cells giving rise to the efferent fibres for the skeletal muscles of the limbs are situated in the anterior horn of the cord. The facts are too well

1 *Archives de Phys. normale et pathol.* 1890, p. 24.

2 *Proc. of Phys. Soc.* (this *Journal*), Jan. 1887, p. iv.

3 Vol. XII. *loc. cit.*

known to need adducing here. The "motor" cells for the intrinsic muscles of the foot are therefore to be looked for in the anterior horn. The anterior horn certainly exhibits most remarkable development in size and apparent complexity in the region in which the great anterior roots are given off to the lower limb. It might appear that the anterior horn at the region of the enlargements of the cord is a compound of two parts. One part equivalent to and continuous with the small anterior cornu that runs with comparatively little modification throughout the entire length of the rest of cord, *e.g.* through the thoracic region. This component in the enlarged horn of the limb regions forms the most medial part, and abuts immediately on the lateral edge of the anterior column. This portion of the horn representing the main bulk of the whole anterior horn of other regions is in the limb enlargements overshadowed by a great lateral appendage to it. That the increase in the size of the horn in the lumbar and cervical enlargements is mainly by excrescence of the lateral edge of it seems indicated by the fact that in the enlargement of the cord the bundles of the anterior rootlets still continue to emerge from about the same somewhat restricted inner piece of the ventral side of the grey matter whence they emerge in other regions of the cord where the anterior horn is of small and simple type. If the point of emergence of the anterior rootlets from the grey matter can be taken as a guide, one may say with little hesitation that the increase in size of the horn in the limb regions is due to the addition of a large lateral mass. Within this lateral mass of the horn in the case of each of the enlargements of the cord, the nerve-cells appear distinctly as two large and well-defined groups. These are the *antero-lateral* and the *postero-lateral cell-groups* of the anterior horn. There is at certain levels also a middle group lying nearer the centre of the horn, but this is far from being so large or clearly defined a group as are the other two. I have examined a large number of preparations of the cord during the past two years with regard to these cell-groups and in respect to their grouping am inclined to believe with Gowers[1] "that the process of distinction has sometimes been carried too far." In the cat, dog, and in Macacus as in man *antero-lateral* and *postero-lateral* groups appear really to be of distinct existence. There are three main groups of cells obvious in the anterior horn of the enlargement, a *medial* continuous with the group that in fairly unbroken fashion extends throughout the entire length of the cord; an *antero-lateral* and *postero-lateral* that are not obvious elsewhere than in the enlargements.

[1] *Dis. of the Nerv. System*, Vol. I. p. 167.

What is the longitudinal arrangement and relationship of these groups? When transverse sections of the cord arranged serially are examined successively in an ascending direction, the cord at the level of the 10th sub-thoracic nerve-root is found to present a small and simple anterior horn, containing but one collection of large cells that could be in bold terms described as a group. Passing upward to the level of the rootlets of the next segment (it must be remembered that here the rootlets form a close unbroken row) a second group with some abruptness makes its appearance in the horn: this is a *lateral* group. It rapidly acquires such proportions as to dwarf the original *medial* group, but it lies quite away from that group and is so large as to cause a prominence which even in the cat is well seen without help from the microscope. Scarcely has this group become well established when another group almost as suddenly appears in the horn, again a lateral group, but lying ventral to the preceding one.

At a higher level still the original *medial* group itself becomes enlarged, but at that level the lateral group which was the earlier met in following the serial sections upwards is much reduced in size, and somewhat higher disappears.

Thus as one passes from below the enlargement into it the first modification undergone by the anterior horn is that the *postero-lateral group* of cells appear. Somewhat higher the *antero-lateral* group is added, higher still the *medial* group of the horn attains its maximal development.

Examined therefore in the ascending direction the cord displays at the same point at which the outflow of efferent fibres to the lower limb begins (and we know that outflow begins with fibres to the intrinsic muscles of the foot) a striking change in the constitution of the ventral horn, owing to the sudden addition to the horn of the great *postero-lateral group* of ganglion cells. This group therefore suggests itself as related to the intrinsic muscles of the foot.

In order to test the point somewhat further I have examined the condition of the cell groups of the anterior horn in an adult cat from which the left hind foot had been removed when the animal was less than a month old. Frontal sections[1] of this cord taken from the level of the 10th subthoracic nerve root shewed no abnormal amount of lateral asymmetry. Sections from the region of the 9th root revealed no indubitable asymmetry until near the junction with the region of the 8th. There as the *postero-lateral group* of the horn appears it is on the left

[1] The sections were shown at a Meeting of the Physiological Society, Feb. 13th, 1892.

side obviously smaller than on the right; not only is the protrusion of the grey matter caused by the group less than on the right side, but it contains fewer ganglion cells, and this becomes still more obvious in ascending to the region of the 8th root. In thirty-five sections taken from the upper part of the region of the 9th root and from the whole region of the 8th the number of ganglion cells (only those containing nuclei being counted) in the three main cell groups of the anterior cornu of the right and left sides was counted and gave the following result.

Posterolateral Group.			Medial Group.		Anterolateral Group.	
Section	Right	Left	Right	Left	Right	Left
1.	6	3	5	4	4	5
2.	7	4	5	6	2	2
3.	5	6	4	3	0	0
4.	5	3	7	4	1	0
5.	8	5	9	10	5	3
6.	4	4	2	4	3	4
7.	12	5	8	7	6	9
8.	8	4	5	2	5	4
9.	7	7	3	7	5	4
10.	7	6	4	3	5	7
11.	6	5	4	5	3	2
12.	9	5	5	2	4	7
13.	8	6	2	7	4	3
14.	10	8	6	3	6	6
15.	7	4	3	4	4	3
16.	7	3	4	1	5	6
17.	4	3	3	5	3	2
18.	6	4	1	6	8	5
19.	18	11	9	7	11	13
20.	10	4	3	4	6	7
21.	16	5	8	3	8	9
22.	9	5	5	4	5	4
23.	7	4	4	7	4	3
24.	13	7	7	2	6	5
25.	8	3	3	5	4	4
26.	5	5	2	1	5	7
27.	8	4	5	1	6	3
28.	6	5	3	5	2	1
29.	11	10	4	4	8	7
30.	12	9	6	2	3	9
31.	7	8	3	6	4	2
32.	11	7	4	3	5	6
33.	9	4	6	3	3	2
34.	9	6	2	6	4	3
35.	8	6	7	5	5	3
	293	188	161	151	162	160

In the region of the 7th root the asymmetry of the anterior horn is not sufficiently marked to be unmistakable, in the region of the 6th the right and left cornua appear of quite normal symmetry. It would seem therefore that the absence of the foot from an early period of life entailed a certain degree of arrest of development of the posterior (lower) end of the postero-lateral cell-group of the anterior horn in the 8th and 9th subthoracic segments of the cord.

Cruveilhier and Türck failed to find changes in the spinal cord or roots follow amputation of a limb. Friedreich[1] also found no change in the cord twelve years after amputation of the forearm. Yet it is now well known that atrophy of the cell groups of the anterior cornu may ensue in result of amputation of a limb, just as arrest of development of part of the oculomotor nucleus ensues after excision of the orbicularis palpebrarum (Mendel).

Bérard in 1829 showed before the Anatomical Society of Paris the spinal cord of a soldier who had had his arm amputated at the battle of Waterloo; the anterior roots of the nerves to the arm were atrophic, but not the posterior, and no change was discovered in the cord.

Vulpian[2] in May 1868 enquired whether after amputation any changes in the cord could be detected similar to some then recently described by Lockhart Clarke in progressive muscular atrophy. He found changes but not similar to the changes in progressive muscular atrophy. Regarding the grey matter, in two cases of amputation close above the left ankle he found that in the lumbar enlargement "la corne antérieure de la substance grise du coté gauche est beaucoup moins large que celle du coté droit." In his figures the contour of the grey matter is most altered at the levels of the 2nd and 1st sacral roots, and it is reduced most where it belongs to the postero-lateral group. This however is not alluded to in his description. At the same time in this country Lockhart Clarke[3] drew attention to asymmetry of the cord existing in two cases of old standing amputation. In one there had been amputation at the left thigh fifty-three years before death. He described in the grey matter of the lower lumbar region atrophy of the left anterior horn "in its lateral region." Clarke's figure shews the antero-lateral cell group little altered, the postero-lateral cell group much reduced. The second case related to amputation at the shoulder. In 1869

[1] *Progress. Muskelatroph.* p. 140.
[2] *Arch. de Physiol. nor. et path.* p. 443.
[3] *Medico-Chir. Trans.* Vol. LI. p. 249. Johnson and Clarke.

Dickinson[1] published observations of a similar kind on 3 cases. He reported a slight loss of bulk in the grey matter on the side corresponding to the lost member; he said no microscopic change in the grey matter was discernible.

Vulpian[2] contributed the first experimental observations. He found that in young rabbits asymmetry of the cord followed section of one sciatic nerve even so soon as two months after the operation. The change he found more perceptible in the posterior horn and columns than in the anterior horns and columns. No details of the effect on the grey matter are given by him. Troisier[3] found in a case of arrested development of the hand and forearm fewer cells in the anterior horn of the lower cervical enlargement on the corresponding side, but the cells were normal. Dickson[4] found in a case where amputation of the right leg had been performed fifteen years before, that the cells in the anterior horn of the lumbar region were fewer on the right than left side. His figures shew that the postero-lateral group was chiefly affected. G. Hayem[5] described the alterations induced in the cord in two young rabbits by tearing out the sciatic nerve. The reduction in the number of cells of the grey matter on the side of the operation was marked. He says "dans toute l'étendue de la substance grise les cellules nerveuses sont atrophiées; cependant on en retrouve presque partout et surtout dans la corne postérieure et l'extrémité antérieure de la corne antérieure. Le point où l'atrophie de ces éléments a atteint son maximum correspond au groupe externe et postérieur de la corne antérieure (tractus intermedio-lateralis)." From his figure it is clear that the tractus intermedio-lateralis is not really meant, but the postero-lateral group. In 1874 Prevost and David[6] examined the cord in a case of old-standing degeneration of the muscles of the ball of the thumb. The only muscular part intact was a portion of the adductor pollicis. In the 8th cervical segment the postero-lateral group of the anterior horn was reduced almost to nil, the anterior and mesial groups of the horn seemed normal. Two years later Hayem[7] reported a case in which he found general atrophy of the anterior horn in the 8th cervical and 1st thoracic segments five years after amputation of the forearm.

[1] *J. of Anat. and Physiol.* p. 88.
[2] *Arch. de Physiol. nor. et path.* 1869, p. 675.
[3] *Arch. de Physiol.* IV. 1871.
[4] *Path. Trans.* London, 1873, p. 2.
[5] *Arch. de Physiol.* 1873, p. 504.
[6] *Arch. de Physiol.* 2nd series, Vol. I.
[7] *Bull. de la Soc. Anat.* 1876, p. 230.

Kahler and Pick[1] noted change in the grey anterior horn in the cervical enlargement six years after amputation of the forearm. They described the postero-lateral group as not particularly affected. No change was found in the 7th and 8th cervical segments. The condition of the first thoracic segment is not mentioned by them. Genzmer[2] reported atrophy of the large ganglion cells in the anterior horn in a case of amputation above the knee of thirty years' standing. In his figure the postero-lateral group appears to have suffered more severely than the antero-lateral; he does not however advert to that point. Passing over observations by Erlenmeyer[3] and by Leyden[4] corroborating the evidence already quoted the next information comes from Deyérme and Mayor[5]. They found in result of amputations of part of the limb a general and equable atrophy of the grey and white matter in the corresponding side of the cord, without diminution in the number of the ganglion cells. In one instance only, namely in a case of amputation of the thigh did they discover in the hind region of the lumbar enlargement for a distance of about one centimetre the number of ganglion cells in the anterior horn reduced by about a third; the reduction affected chiefly the medial group. Dreschfeld has recorded[6] atrophy of the anterior horn in the lumbar enlargement in a case of amputation above the knee; the diminution in the ganglion cells affected all the groups of the horn, especially the 'intermedio-lateral" by which from the figure is evidently meant the postero-lateral of the anterior horn. W. Dudley has given a like case.

L. Edinger[7] examined the cord in a case of intrauterine amputation of the left hand, accompanied by some atrophy of the forearm. He found marked atrophy in the left anterior horn from the lower end of the 3rd cervical segment to the 2nd thoracic segment. The atrophy was greatest in the antero-lateral and postero-lateral groups of the 6th and 7th cervical segments. Erlitzky[8] noted after amputations in young dogs diminution in the number and in the size of many cells of the anterior horn of the corresponding side. H. Sahli[9] examined a

1 *Arch. f. Psych.* x. p. 360.
2 *Virchow's Archiv*, 1876, p. 265.
3 *Ueber das cicatric. Neurom.* Greifswald 1872, p. 38.
4 *Klinik der Rückenmarks-Krankheiten* II. p. 315.
5 *Comptes rendus*, 1878, xxx.
6 *Journ. of Anat. and Physiol.* 1879, xiv. 424, and Dudley, *Brain*, ix. 87.
7 *Virchow's Arch.* LXXXIX. p. 46, 1882.
8 *Peters. med. Woch.* 1880, p. 38, and Homén, *Ziegler's Beitr.* 1890, 304.
9 *Deutsch. Arch. f. klin. Med.* p. 33, 1883.

case in which the muscles of the right hand and the pronator radii teres of that side were atrophic or undeveloped. The right ulna was shorter than the left. He found a long scar in the cord from the 4th to the 7th segment inclusive; the most marked atrophy was in the postero-lateral cell group of the horn, in the 6th and 7th segments.

In five instances of old-standing amputation of the lower limb C. Friedländer and F. Krause[1] detected in the corresponding half of the spinal cord diminution in size of the posterior white column and of Clarke's grey column and of the anterior grey horn, especially of the postero-lateral cell group. From this observation they drew the conclusion that Clarke's column and the postero-lateral cell group of the anterior horn are both *sensory* in function and are both related to the sensory roots coming from the lower limb.

The above pathological evidence on the whole bears out the view advocated here, viz. that of the cell-groups of the ventral horn in the sacral region the *medial* and the *postero-lateral* are connected respectively with axial, *i.e.* spinal (root of tail, &c.) muscles and with the muscles of the sole. It also suggests the occurrence of a similar relation among the cell-groups of the ventral horn in the cervical enlargement. The scope of the enquiry has therefore been extended to the cell-groups and nerve-roots of the cervical region as well.

The anterior horn in the cervical enlargement, just as in the lumbar, exhibits three main-cell groups, a *medial*, an *antero-lateral*, and a *postero-lateral*. A central group also exists and is more definite than is that of the lumbar region. Of these groups the medial, just as does that of the lumbar enlargement, appears continuous with the main part if not with the whole of the small anterior horn of the upper thoracic and upper cervical regions. As in the lumbar enlargement so in the cervical the great increase in size of the anterior horn in comparison with the size of the horn in the adjacent regions seems due to a lateral addition to it, a lateral excrescence from it, of a part not present, or scarcely present in the adjacent regions above or below. This lateral part is therefore obviously related to the limb.

In the cervical enlargement even more obviously than in the lumbar, as the conformation of the horn is studied in a series of sections followed in an ascending direction, the earliest cell-group to appear, that is to say the group which extends farthest in the posterior or downward direction, is the great *postero-lateral*; that cell-group suddenly springs into prominence. Where? Of two Rhesus cords examined

[1] *Fortschritte der Medizin*, Vol. iv. p. 749. 1885 Dec.

with special reference to this point, in one it first appears just midway between the 2nd and 1st thoracic nerve-roots; in the other in the sections from the 1st millimeter of the distance between the 2nd and 1st thoracic roots counting from below upward.

It has been shewn above that in Rhesus and in Bonnet the lowest fibres to the limb muscles leave by the 2nd thoracic root. In the case of the second of the two Rhesus cords examined, I knew by experiment that the 2nd thoracic supplied the intrinsics for the hand unusually liberally and it was for that reason that the cord was preserved for microscopical examination. In the upper limb therefore as well as in the lower an agreement holds between the position of the outflow of efferent fibres to the intrinsic muscles of the distal segment of the limb and the position of the *postero-lateral cell group* of the anterior horn.

In the transition from the upper thoracic region to the cervical enlargement the change of conformation undergone by the grey matter of the cord is not quite comparable with that exhibited in the transitions at the lower end of the lumbar enlargement. There is no indisputable *lateral horn* among the components of the cord in the latter region. In the former region of the cord the *lateral horn* is a salient feature.

At the level of the 3rd thoracic nerve-root the lateral horn is the well-known sharp tapering spike thrust sidewise from the grey matter in front of the lateral reticular formation with a slight inclination forwards into the white lateral column. The spike contains the numerous small oval and angular ganglion cells, originally described by Lockhart Clarke[1]. The major axes of the cells are directed for the most part so as to radiate into the lateral column. Where the lateral horn is well developed members of the group frequently lie outside the confines of the grey matter on radiating strands which penetrate the lateral column[2]. Not unfrequently in sections from the levels of the 8th and 9th sub-thoracic roots the ventral part of the lateral reticular formation displays a group of small spindle-shaped ganglion cells resembling many in the lateral horn of the thoracic region, and in the reticular formation in all regions. Whether these cells represent a lateral horn or no is difficult to prove. Gaskell[3] has shewn that numbers of fine efferent fibres exist in the anterior roots of the 1st and 2nd sacral just as in the

1 L. Clarke. *Phil. Trans. R. S.* 1851. Part II. p. 613. Also *ibid.* 1858, p. 439.

2 Sherrington. *Phil. Trans. R. S.* 1890.

3 This *Journal*, Vol. VII.

roots of the lateral horn region of the cord. Waldeyer[1] mentions the group with special reference to the origin of the small efferent fibres discussed by Gaskell, but he abstains from any definite conclusion with regard to the group.

Although the size of these small ganglion cells varies somewhat, all of them may be said to be "small," they perhaps would vary in size less were it possible to eliminate the source of fallacy of measuring individual cells in which one extremity may have been partially truncated by the plane of either a longitudinal or a frontal section. I give the length and width of twelve individuals measured from the cord of Rhesus without selection in three preparations at the 3rd thoracic level (bichromate hardening and dehydration).

	length	width		length	width
1.	34·5 μ	18 μ	7.	33 μ	12 μ
2.	23·5 ,,	15 ,,	8.	30 ,,	16 ,,
3.	32 ,,	12 ,,	9.	26 ,,	13 ,,
4.	27 ,,	17·5 ,,	10.	37 ,,	22 ,,
5.	23 ,,	14 ,,	11.	24 ,,	12 ,,
6.	31·5 ,,	18 ,,	12.	28 ,,	16 ,,

If to these are added some measurements from examples in the adult human cord at the level of the 6th thoracic an average length of 33 μ is given for twenty-two measurements. The average width in twelve measurements is 15·4 μ. These dimensions are smaller than the average given by Waldeyer's five measurements, namely, $42\,\mu \times 21\,\mu$. By searching the lateral horn in a series of preparations one easily finds individual cells of smaller measurement than any of the above, and some that are larger. The largest are about twice the size of the smallest. In shape the cells whether large or small all closely agree, varying from wide to narrow ovoids. Mott[2] has recently adverted to the cells as occurring in two sizes, a smaller kind averaging 20 μ, a larger 30 μ. There certainly are both larger and smaller cells in the horn (the largest being as already said quite twice the length of the smallest) but there are also I incline to think many of sizes intermediate as well. I am doubtful therefore whether this forms sufficient basis for a subdivision of the group.

The spongiosa of the lateral horn, in which the cells lie imbedded, exhibits a peculiarity not mentioned, I think, in any published descrip-

[1] *Gorillarückenmark* 1889.

[2] Bipolar cells of the Spinal Cord, *Brain*, 1891.

tions of the horn. The grey matter of the cord reveals to the gold method and to the Weigert or Weigert Pal hæmatoxylin methods, a now familiar wilderness of fine fibres complexly interlaced throughout the spongiosa. But the richness of the feltwork of fibres is not equally great in all districts of the grey matter. In a cross section of the thoracic cord the fine fibres are more numerous in the anterior horn and in Clarke's vesicular cylinder than in the grey matter elsewhere; the feltwork is, as is well known, closest in the vicinity of the great ganglion-cell groups; usually round these groups twists so to say a torcula of fibres. The group lies nested at the focus of a rude ellipse of fibrils. Often the number of fine fibres actually amid the cells is not so great, but the number of fibres edging the group is always large. The ventral horn, especially in the enlargements, affords excellent illustrations of this point, and no more striking example of it can be found than in the cell group of the hypoglossal nucleus of the grey matter of the bulb. One has only to hold up against the light a Pal-Weigert frontal section of the bulb in the region of the XIIth nucleus to see with the unaided eye the dark tinging of the grey matter marking out that nucleus from the rest of the grey matter round about: by the microscope that tinging is resolved into a network of fine fibres richer at the nucleus than elsewhere. With the spongiosa of the lateral horn and its included group of numerous ganglion cells the case is different; within it the network of nerve-fibres is extremely sparse; I incline to think it possesses a far sparser content of fibres than any other portion of the grey matter, excluding the regions of the gelatinosa centralis and posterior. Indeed with regard to it the reverse of what was stated above holds true; instead of being swathed by a fibre network denser than elsewhere, the *lateral horn group* is rendered conspicuous by the dearth of nerve-fibres in it and about it; in Weigert preparations it often stands out from the rest of the grey matter even to the naked eye as a point of a clear yellow tint undarkened by the hæmatoxylin stain. Examined with the microscope there is not that whirl of fibrillæ sweeping round the cells so characteristic for the cell groups of other districts.

It may be noted in passing that this feature constitutes a remarkable point of similarity between the spongiosa of the lateral horn of the thoracic region of the cord and the spongiosa of the Xth nucleus (vagus nucleus) in the bulb. I note the resemblance here because it bears on the suggestion of Gaskell[1] with regard to the functions of the

[1] This *Journal*, Vol. VII. and Mott, *Brain*, XIII. 433.

lateral horn and because it contributes to the resemblance between the lateral horn of the cord and the vagus nucleus of the bulb on other characters of which I have already laid some stress elsewhere[1].

The lateral horn of the 3rd thoracic segment characterised by its spindle-shaped nerve-cells averaging 33 μ in length and by the relative paucity of its nerve-fibres is found in the two Rhesus cords but little altered as far up as the middle point of the superficial origin of the 2nd thoracic root. In the sections taken from the 2nd millimeter above that point it becomes altered, the alteration consists in the appearance of some large cells in the lateral horn at its base. (Figs. 10 and 11, Pl. XXI.) These large cells measure far more in length (90 μ) and breadth (40 μ) than do any cells in the horn of the 3rd and 4th thoracic segments of the cord. There is still a numerous collection of the small ovate cells in the horn just as at lower levels, so that the comparison is easily made between the cell group already present in the horn and the large new comers juxtaposed to them.

The change thus inaugurated is rapidly accentuated as the horn is followed upward. At a level half-way up the region of the superficial origin of the 1st thoracic root the large ganglion cells have increased to a great group; they are collected first in the ventral portion of the base of the lateral horn, and then extend in a lateral direction into the lateral column, causing excrescence of the most dorsal portion of the lateral edge of the anterior horn. The excrescence extends far enough in the dorsal direction to merge with the old lateral horn, so that at the 1st thoracic root there is one part, the dorsal edge, of the new excrescence which is representative of the whole lateral horn of the 2nd thoracic and lower levels.

This view is borne out by there being in sections from as high as half-way up the superficial origin of the 1st thoracic rootlet, small spindle-shaped nerve-cells similar to those typical of the lateral horn occupying a place in the dorsal edge of the excrescence caused by the new large cell group. Above the 1st thoracic nerve the small cells seem to quite disappear, and the last remnant of the lateral horn goes with them, for the spongiosa of the new excrescence is not like that of the lateral horn or that of the vagus nucleus but like that of the anterior horn of the cord. The group of great nerve-cells which thus abruptly springs into existence at the level of the 2nd thoracic in Macacus root is when traced upward found to be the *postero-lateral group* of the cervical enlargement.

[1] *Phil. Trans. R. S.* 1890, B. p. 33.

The above description will be found somewhat different from that given by Schwalbe[1] and from that given by Waldeyer[2].

Schwalbe divides the cells of the anterior horn of the cervical enlargement into two groups, a mesial and a lateral. He writes that the lateral group of the anterior cornu extends so far back into the base of the horn that a delimitation of it from the group of the lateral horn is not possible, and the question must remain open as to whether the lateral horn cells are absent in the enlargement or whether they become fused into one group with or converted into the cells of the lateral group of the anterior horn; the latter possibility he considers the more probable.

Waldeyer in his description of the grouping of the cells in the cord of gorilla says that the lateral horn cells are found throughout the cord in all its segments, including those of the cervical and lumbar enlargements. He divides the ganglion cells of the cord into as many as fourteen definite groups, attaching to each a name, but treats the cells of the lateral reticular formation and those of the lateral horn as one group (Mittelzellen). When he says that the cells of the lateral horn are present in, for instance, the 8th and 7th cervical segments his meaning is that there are cells in the reticular formation at that level which he considers are cells of the lateral horn, although that horn can no longer with certainty be recognised. But in regions where the lateral horn exists there are cells in the lateral reticular formation as well as in the lateral horn, and the assumption that the cells of the lateral reticular formation although somewhat similar to the cells of the lateral horn are identical with them, or are their equivalents, is a somewhat insecure foundation on which to rest the statement that the cells of the lateral horn are present in a region where there is no other evidence of them beyond cells in the lateral reticular formation. It is not foreign to the argument here to note that Waldeyer considers that not only the cell group of the lateral horn is really present throughout the whole of the length of the spinal cord but that the cells of Clarke's column are in like manner present really throughout the cord in its entire length. However interesting may be the speculation that into each link of the whole chain of segments forming the cord the same elementary factors of morphological composition enter though here and there one factor or another be difficult to trace, the speculation loses much interest if not placed on a basis of demonstrable fact. In the

[1] *Neurologie.*

[2] *Gorillarückenmark.*

adult cord of the cat, dog, macaque and man there is no clear evidence that cells of Clarke's column do extend throughout the whole length of the cord in every segment of it. Myself I hold[1] that in one category with Clarke's column should be included all those cells which lie on the bundles of the posterior roots in their intraspinal course whether in the posterior horn or in the posterior column. Yet even then one's own preparations have failed to shew indubitable members of the group in, for instance, the 6th and 7th sub-thoracic segments of the adult cord, nor have I ever met with them in numerous preparations of the 7th cervical segment.

Gaskell[2] describes the cells of Clarke's column extending as a distinct group along the cord of the Dog from the 9th segment to the 25th; Mott examining the column in Dog, Macacus and Man, describes it as extending in all three from the 9th to the 22nd segments only. My own observations agree completely with the above as to the upper limit of extent of the cell group, but not as to the lower. There I find a distinct difference between Dog and Macacus and Macacus and Man. The following countings give the average number of cells observed in not very thin microscope sections of the cord at the levels mentioned, each average being taken from not less than five sections counted at each level.

Number of cells in Clarke's column.

No. of spinal segment.	Dog.	Macacus.	Man.
9th to 18th	1—5 cells	1—7 cells	1—8 cells
19th	3·6	4·3	7·7
20th	4	5·3	7·4
21st	4·2	6·4	10·3
22nd	5·3	6·1	8·2
23rd	5·7	3·4	0·9
24th	5·4	0·6	0
25th	3·8	0	0
26th	·7	0	0
27th	0	0	0

For the Dog the lower limit of the cells as a group is practically the same as that described by Gaskell. In the cord of the newly-born puppy and of advanced fœtus of Rhesus the group does not appear to end so abruptly below as in the adult and is continued in a straggling manner into segments even below the 26th.

[1] *Phil. Trans.* 1890, *loc. cit.*

[2] This *Journal*, Vol. VII. *loc. cit.*

In the same way I have been unable to convince myself in spite of the examination of numerous preparations, that the lateral horn group is really present in the cervical enlargement of the cord at all higher than the middle of the superficial origin of the 8th cervical nerve; once, in the cat, I have met with doubtful instances of them as high as that. In Rhesus I have not found them above the surface origin of the 1st thoracic root.

My conclusions from my own specimens are

(1) That followed in an ascending direction the lateral horn and its cell-group fails somewhat abruptly close above the region of origin of the 1st thoracic nerve-root.

(2) That of the cell groups characteristic of the anterior horn in the enlargement the one which extends farthest along the cord in a descending direction is the *postero-lateral*, and that it reaches to and into the 2nd thoracic segment and there, somewhat abruptly, fails.

If these conclusions be correct there is in the 2nd thoracic segment, of the cord, an overlapping of two different nervous cell systems, a system of the anterior cornu, a system of the lateral cornu[1]. Is there evidence of a physiological as well as an anatomical overlap of systems in these segments of the cord? Most distinctly there is.

Excitation of the anterior root of the 8th cervical nerve causes movements in the limb, contraction of a large number of the limb muscles, but has no effect on the pupil, eyelids, pinna, or hair, in short it gives limb effects but not sympathetic effects. Again, excitation of the anterior root of the 3rd thoracic nerve never, so far as I have seen, causes contraction of any muscle in the limb, but produces dilation of the pupil, separation of the palpebræ, erection of the hair of the scalp, retraction and paling of the pinna, and vaso-constriction in the lobe and half of the isthmus of the thyroid body.

In a summary of the functions of the cervical sympathetic of the Macacque given in a previous paper I omitted to include *vaso-constriction in the thyroid gland*, a phenomenon well marked and constantly obtained. In the rabbit, cat and dog similar vaso-constriction in the thyroid occurs on excitation of the anterior root of the 3rd thoracic.

The motor functions of the 2nd thoracic root examined thirteen times in Macacus, in ten instances gave flexion of the fingers and pollex, with adduction and opposition of the latter, and also flexion at the wrist and pronation of the hand. The movement obtained was

[1] Sherrington. *Proceedings of the Physiological Society*, Feb. 13, 1892.

very slightly altered by section of the ulnar nerve at the wrist, but was much impaired though not abolished by section of the ulnar behind the inner condyle. In three instances the root gave only the movement described for it by Ferrier and Yeo, namely interosseous flexion of the digits, and this was almost completely abolished by section of the ulnar nerve at the wrist; in one of these instances the movement yielded by the excitation was almost confined to the little, ring and middle fingers.

That these results of excitation of the 2nd thoracic are not attributable to escape of the stimulating current to the adjacent root is shewn by the facts (i) that it is possible to obtain similar results reflexly in reply to mechanical excitation after the 6th 7th 8th and 1st thoracic roots have been divided; (ii) that flexion of the digits and flexion and pronation of the wrist are elicitable from the cortex after section of the same roots; (iii) that flexion of the digits and pronation of the wrist can be performed voluntarily after section of the same roots.

Also in the rabbit and rat the 2nd thoracic invariably causes contraction in the muscles of the fore-foot; in the cat and dog very rarely if ever so.

Together with these motor effects in the musculature of the limb excitation of the 2nd thoracic root produces marked 'sympathetic' effects, very similar in Macacus to those already mentioned for the 3rd root. The palpebral and pupillo-dilator changes are striking—more so than in the case of the third root, the pilomotor effect may be good. The vaso-constriction in the lobe of the thyroid body is less evident than in the case of the third and fourth roots.

Again, if the anterior root of the 1st thoracic nerve be excited in Rhesus the effects which follow without exception so far as I have observed are flexion of the wrist toward ulnar side, pronation at the wrist, flexion of the digits, a bringing together of the fingers and hallux and extension at the elbow-joint; and together with these limb movements dilatation of the pupil.

But to compare accurately with one another the mutual longitudinal overlaps of the morphologically differing cell-groups and of the functionally differing nerve-fibres, it is especially desirable to ensure a correct localisation of the extreme upper end of that class of sympathetic efferents which extends furthest into the limb region. This class of fibres consists of the eye-fibres of the sympathetic. Langley has shewn this for cat and rabbit, and they often in monkey extend a segment higher than do the pilo-motors for the scalp.

Since Langley[1] has so recently described the root origins of the cervical sympathetic in the cat, dog, and rabbit, I shall confine the account of my experiments to the root origin of the eye-fibres of the sympathetic in Macacus rhesus. The only previous experiments in the monkey on nerve-roots causing dilatation of the pupil appear to be those recorded by Ferrier in 1883[2]. In them the 8th cervical and the highest four thoracic roots were excited with tetanizing currents in five animals. Dilatation was obtained only from the second thoracic root and in that root only in two out of the five experiments.

In my own experiments excitation shewed the presence of eye-fibres in the 1st, 2nd and 3rd thoracic roots, chiefly in the 2nd, a result in accord, so far, with Ferrier, and in complete agreement with the excitation results recorded by Langley in the rabbit. The action of these roots was not confined to dilatation of the pupil, but gave opening of the palpebral fissure, etc. as described by me elsewhere[3]. The shortness of the piece of nerve-root available for excitation in this region of the cord caused me some anxiety in the experiments since the apparently long range of outflow for so small a muscular district might perhaps be an erroneous estimation explicable by escape of the stimulating current. The objection had the more weight with me because as pointed out by Ferrier the strength of the stimulating current used on the nerve roots has to be considerable in order to obtain eye effects. I therefore as precaution took other observations in which the use of stimulating currents was avoided. Rhesus was anæsthetised, and then after a heavy injection of chloral, one or other of the first four thoracic nerve-roots was exposed and divided in the spinal canal. The pupils of the two eyes were compared as to size by the pupillometer. This mode of testing for the presence of pupillo-dilators proved itself far more delicate than I had anticipated (Fig. 13, Pl. XXI.). Eight observations made in this way yielded perfectly concordant results. I give two examples from the protocols.

2. xi. 91. Rhesus macacus. ♂

Chloral hydrate, than A. C. E. mixture.

10.18	Pupils equal size.		
10.20	1st thoracic root of right side cut.		
10.30	r pupil < l	r = 4	l = 5
11.2	r pupil < l	r = 4	l = 5

[1] *Proc. Roy. Soc.* 1892. Vol. L. p. 447 (Abstract).

[2] *Proc. Roy. Soc.* p. 229.

[3] This *Journal*, Vol. XII.

11.5 2nd thoracic root of right side cut.

11.15 r pupil < l r = 2·5 l = 5

11.30 r pupil < l r = 2 l = 5

11.35 2nd thoracic root of left side excited with secondary at 48 cm. distance from primary (1 Daniel in primary). Gives flexion of fingers, thumb and wrist, and pronation of wrist, weakened but still present after section of ulnar nerve at elbow.

22. iv. 91. Rhesus macacus. ♀[1]

Chloral hydrate, then A. C. E. mixture.

6.12 Pupils equal size.

6.15 4th thoracic root cut on right side.

6.25 Pupils equal size.

6.30 Pupils equal size.

6.33 3rd thoracic root cut on right side.

6.40 r pupil < l r = 4 l = 4·5

6.50 r pupil < l r = 3·5 l = 4·5

6.59 2nd thoracic root cut on right side.

7.10 r pupil < l r = 2 l = 5

7.30 r = 2 l = 5

It is clear therefore that in Rhesus abundantly in the anterior root of the 2nd thoracic nerve and markedly in that of the 1st thoracic there is a demonstrable admixture of two sets of fibres whose purposes though both efferent belong to physiological classes quite distinct. This admixture is not found in the adjacent roots above and below those two thoracic nerves. It is due to the outflow of efferent fibres to the limb muscles extending far enough posteriorly (downward) to overlap the anterior or upper end of the outflow of the efferent fibres of the sympathetic system. It seems reasonable to connect this overlap of the efferent nerve fibres of two different systems in the 1st and 2nd thoracic nerve roots with the above described overlap of two different sets of cells in the grey matter in the same two segments of the cord, especially since the cells of the anterior horn are known to give rise to efferent nerve fibres to the limb muscles and since Gaskell has already suggested the probability that the small efferent fibres of the sympathetic are connected with the cells lying within the lateral horn. It is with a view to contributing toward his suggestive arguments that I state at the risk of being wearisome the details and coincidence of the above double anatomical and physiological overlap existing in these upper thoracic segments.

[1] From this experiment the sketch (Fig. 13, Pl. XXI.) was taken by Mr Lapidge.

It remains to be admitted that the scheme of distribution to musculature of the cell-groups of the anterior horn for which I contend is not in agreement with one advanced by Ross, who has entered fully into the question of spinal localisations in his well-known *Diseases of the Nervous System*[1]. Ross concluded from observations on the time of appearance of the cell-groups that in both the cervical and lumbar enlargements the *antero-median* group belongs to the small muscles of the digits, the *postero-lateral* group to such muscles as the sternomastoid and trapezius. More recently an excellent monograph has appeared on 'Die Funktionen der Ganglienzellen des Halmarks' by O. Kaiser.[2] In it from comparison of microscopical preparations of the cervical region of the cord with the results, chiefly those of Forgue and Lannegrace, of excitation experiments on the brachial roots the author draws among others the following conclusions: "Das Halsmark enthält die folgenden Gruppen: i. der Rückenmuskelkern erstreckt sich als mediale Säule durch die ganze Länge." "ii. der oberextremitätenkern liegt lateralwärts; die distal Hälfte zerfällt in eine vordere und eine hintere Abteilung—erstere innerviert Adductoren des Oberarmes, und den Triceps, leztere Benger und Strecker der Finger, ulnar Muskeln und die kleinen Muskeln der Hand." These conclusions as regards the postero-lateral group agree completely it will be seen with the evidence afforded above and perhaps best of all by Prevost and David's case. With regard to the medial group and the postero-lateral group the conclusions are the same for the cervical region as that to which my own observations have led me in the lumbo-sacral region, as well as in the lower cervical. To the overlap of the cell systems, or therefore to its physiological significance Kaiser does not it is true advert; he remarks only, "was endlich die Zellen des Mittel und Hinterhornes betrifft so sind diese wohl zum grossen Teil als reflex übertragende und regulatorische Centren anzusehen."

The conformity of the mutual longitudinal overlap of the cell-groups of the *lateral horn* and *postero-lateral* region of the ventral horn, with the mutual longitudinal overlap of the outflows of sympathetic efferents and motor nerves to the digits enhances the probability of the '*sympathetic*' nature of the lateral horn cells and of the view above advocated as to the connection of the postero-lateral cell-group of the anterior horn with the muscles of the palm and of the sole.

[1] Vol. ii. [2] Hannover. Dec. 1891.

It is here worthy of remark that one finds the lateral horn a distinct feature of the cord so low as the region of surface origin of the 4th lumbar nerve, but in the region of the 5th its presence cannot be affirmed with certainty, it is at any rate not distinct. I fail in either of two Rhesus cords examined to detect its presence with certainty below the 6th millimeter from the top of the region of surface origin of the 4th lumbar root. It has been shewn above that the 4th lumbar root (but not the 5th) contains efferent fibres to the bladder which reach that viscus by way of the *sympathetic*. Here also the correspondence of locality is therefore striking.

A further point may be mentioned. The posterior or inferior end of the long postero-lateral cell-group of the lumbar enlargement is relatively longer and more prominent in the cord of Rhesus than in the cord of cat or man. This, on the view that it belongs to the intrinsics of the foot, becomes explicable by the greater freedom of movement of the digits in the foot of Rhesus than in the foot of man or cat. Again in the 9th and 10th subthoracic segments the medial-group is poorly developed in man as compared with Rhesus and the Bonnet; from these segments proceed in the latter animals the efferent nerves to the muscles of the root of the tail, and we saw reason to suppose that the motor nerve fibres for spinal muscles arise from the medial cell-group of the anterior horn. The medial group pertains to axial muscles.

Although both in Rhesus and Cat the appearance of the postero-lateral group is the most evident change in construction in the anterior horn at the levels of origin of the 9th and 8th subthoracic roots, an alteration in the medial sub-group does also occur there. The medial cell-group there becomes absolutely larger though not relatively so in comparison with the whole horn. It is indeed a well-marked group in the region next below the levels now under discussion, but it seems to become rather more marked at these levels. Were it to this group rather than to the postero-lateral that the intrinsic muscles of the foot belonged, we should not expect to find the medial group well developed in segments to which belong no limb muscles at all; further, the muscles belonging to the proximal portion of the tail are, both in Rhesus and Cat, well represented in the same segments of the cord as are the intrinsic muscles of the foot; and the muscles of the root of the tail are more powerful and also one would think more used than those of the distal part of the tail. So that, supposing the mesial cell-group of the anterior horn of this region of the cord to be related to the tail muscles it might be expected that the group would be present in the

9th—8th segments of the cord and in well-developed proportions. And it was seen that after loss of the distal member of the limb the mesial cell-group did not shew good evidence of ill development.

The above argument for a connection between the lower end of the postero-lateral cell-group of the anterior horn and the intrinsic muscles of the sole and palm has proceeded all along on an assumption that seemed so natural I have forborne discussing it as early as perhaps should have been really done. This assumption is that a major part of the fibres of the rootlets composing the anterior division of the root of a spinal nerve is derived from nerve cells in the grey matter of that segment to which the particular anterior root in question is attached by its superficial origin. This assumption has been made so generally that I can find but little evidence recorded either for or against it.

L. Edinger[1] after examining the condition of the spinal roots in the case of intrauterine amputation of the hand already referred to pointed out that as the atrophy of the roots was greatest at the same level as the greatest atrophy of the cells the chief part of the nerve fibres of the brachial plexus must arise in the grey substance of the cord at the same level as their place of attachment to the cord.

But in the case of a posterior root although some portion of its fibres appear to possess end stations in the grey matter of that segment to which its filaments are attached, it is certain that very considerable portions of its fibres first reach end stations in segments far distant above the segment at which they began an intraspinal course.

It might be judged from the long sloping course of the anterior roots in the cauda equina that an almost longitudinal direction would be for some distance maintained by the fibres of the rootlets intraspinally. In reality such appears not to be the case or to a very slight extent only. For instance in the region of exit of the long slanting sixth subthoracic nerve rootlets, frontal sections will sometimes display one and the same anterior root-fibre crossing from a point in the grey matter abutting on one of the cell-groups of the horn right away to a point in a bundle of anterior root-fibres close to its emergence at the periphery of the white antero-lateral column. In some frontal sections I have seen one and the same anterior root-fibre traceable from close to the medial side of the postero-lateral cell-group of the anterior horn away into an anterior root bundle and along that for nearly the whole length of it; the fibre in these cases extends more than half across the section of the cord. Very notable is the bold sweep with which such

[1] L. Edinger. *Virch. Archiv*, LXXXIX. Bd. 1882.

fibres traverse the grey matter intervening between the cell-group whence they come and the root bundle into which they pass. They emerge from the postero-lateral cell-group only a fraction of a millimeter above or below the point of their emergence at the surface of the cord.

Wishing to test somewhat more closely this question respecting the relative positions of the superficial and deep origin of the anterior roots I divided the cord of Rhesus completely across close above the 9th thoracic nerve-root, and then examined the condition of the fibres in its rootlets four months later. I found them to contain, even the most anterior (highest) of them a large number of sound nerve fibres (Fig. 12, Pl. XXI.). The sound nerve fibres were both of large and small diameter, the smaller being evidently those described by Reissner[1] and Gaskell[2] and ascribed by the latter to efferents going to the sympathetic system. It might be objected that at the level of the 9th thoracic root that slant of the root-fibres after their exit from the cord so characteristic in the lumbar region hardly exists, and that therefore the result obtained may not be applicable to the roots of the lumbar region. To meet this the above explanation that the slant is almost purely extraspinal not intraspinal may be cited, and the following observation. The spinal cord of Macacus rhesus was completely divided across just under the origin of the lowest thoracic nerve-root, and again, as later examination shewed, not quite completely, part of the left anterior column escaping, at the origin of the 3rd lumbar root. Time was allowed for degeneration to occur (six months was allowed). The anterior root of the 1st lumbar was then stimulated by weak tetanising currents and gave smart contraction of the muscles of the abdominal wall; one side only was tested, the other being left undisturbed for the sake of subsequent microscopic examination. The 2nd lumbar nerve anterior root also gave smart contraction in abdominal wall on excitation. The 12th thoracic and the 3rd lumbar roots gave no contraction; the lower section wound was found to traverse the origin of the 3rd lumbar root about its widest part; the root of the 12th thoracic was found to have been divided in its extraspinal course in the performance of the transverse division of the cord just below its place of origin. The anterior root of the 4th lumbar gave contraction in the upper muscles of the front of the thigh, with slight flexion of hip and slight extension of knee with adduction.

The 1st and 2nd lumbar, and the 4th lumbar anterior roots were

[1] *Archiv f. Physiol.* 1862, cf. also Beck, *Phil. Trans.* 1846, p. 213.
[2] This *Journal*, Vol. VII. *loc. cit.*

preserved for microscopic examination. In all three there are large quantities of perfectly sound medullated nerve-fibres, both of large and small calibre. It is difficult to affirm that any fibres have disappeared, but the connective tissue in the 1st and 4th lumbar roots appears to be excessive, especially in the last mentioned.

SECTION V.

THE SIGNIFICANCE OF THE ARRANGEMENT OF THE LIMB-PLEXUS.

The functional significance of the limb plexuses and of the muscular arrangements represented in the nerve-roots deserves consideration.

Enough has been said in the short historical review given at the beginning of this paper to shew that from the commencement of this century there has been division of opinion concerning the significance of the nerve-plexuses of the limbs. On the one hand it has been supposed that the origin of their existence lies in the functional necessity for associating to one cell-group in the cord muscles placed apart from one another in the limb; this view was based on the observation that muscles placed widely apart are contemporaneous in action even in simple movements of the limb, and on the belief that the individual cell-groups of the cord representing the spinal nervous centres were of transverse rather than longitudinal extent. Against this we know that most movements are represented in vertical tracts and that the whole anterior grey matter at any one nerve-segment contains cells that are concerned with a number of different movements[1].

As mentioned above, Panizza and also Kronenberg declared a chief use of the plexal arrangement of limb-nerves to be protection of the muscles against fatigue. An experimental test of their hypothesis they do not seem to have supplied. I have for various reasons attempted to offer one. The view, old though it be and somewhat crude though it appear as briefly stated in the "Essay" of 1836, harmonises with the modern doctrine that the nature of the movement produced by excitation of a single spinal root is highly coordinate, for the use of the plexus might be that one part of a muscle should be employed in some particular coordinate action without drawing upon the resources of another part of the muscle to be brought into play fresh in some other particular coordinate action. The test experiment might also throw some light on the existence of the 'fatigue substance'

[1] Cf. Gowers. *Diseases of the Nervous System*, I. p. 128.

supposed to be related to peripheral fatigue. The method by which I attempted a test of the matter may be perhaps best stated by briefly relating an experiment.

May 2, 1891. Rana temporaria, ♂. Pithed at 9.40. Right gastrocnemius tendon isolated and fixed in myograph, femur and crural bone had been previously clamped to platform. Circulation intact, the peroneal and all branches of the sciatic cut in thigh except the popliteal. The vii, viii, and ix roots ligated just outside the intervertebral foramina and then divided proximal to the ligatures. The three roots are freed from the strands of connective tissue tying them somewhat together; the completely free part of the viii root has a length of 19 mm., the length of the vii root somewhat exceeds it, that of the ix root is somewhat less. Each of the three roots is laid on a pair of platinum electrodes, the points in each pair being 1 mm. apart. The myograph is arranged for isotonic contraction, a load of 25 grms. is attached to the lever at 2 mm. from the lever's axis. The electrodes connected with the viiith root are those of the secondary coil of the sliding inductorium with Helmholtz side wire, in the primary circuit a one pint Daniell's element. The position selected for the secondary coil is one at which muscle-nerve preparation is found to give a submaximal contraction with both make and break shocks. The electrodes upon which the ix root is placed are those of the secondary of a similar inductorium in the primary circuit of which a one pint Daniell is the element. A rotating key is introduced into both the primary and secondary of this inductorium so that breaking shocks only are conveyed into the nerve root connected with it. Further it is arranged that after a certain number of break shocks have been thrown in by the electrodes, the break as well as the make shocks shall be for a time cut off from the electrodes by a short circuiting key. A switch is also introduced into this secondary circuit, allowing the current into the electrodes on which the vii root is placed if desired. Time marker indicates each twenty-fifth second. Recording surface travelling 2 mm. per second.

9.58. Break current switched from root ix into vii gives good contraction of sartorius and rectus but no trace of contraction in gastrocnemius. Break current thrown into root viii gives no contraction in sartorius and rectus.

10.1. Make and break currents from rotating key thrown into root viii give make contraction of 42 mm., break of 47 mm.

10.2. Ditto after interval of 114″ give make contraction 44 mm., break 47 mm.

10.3. Ditto after similar interval, make contraction = 44 mm., break 47 mm.

Then 136 contractions (break) through root ix in 55″, then 5″ pause. Then make contraction through root viii = 44 mm. 9″ pause, then break contraction through root viii = 47 mm. 7″ pause.

Then 136 contractions through ix as before, no evidence of "fatigue" (Fig. 15). 5″ pause. Make contraction through viii = 44 mm. 9″ pause. Break contraction through viii = 47 mm. 7″ pause.

Then 136 contractions through ix as before. Evident diminution of height of contraction 5″ pause. Make contraction through viii = 41 mm. 9″ pause. Break contraction through viii = 44 mm. 7″ pause.

Then 136 contractions through ix as before. Marked evidence of "fatigue." Contraction height reduced to less than $\frac{1}{3}$ (Fig. 15). 5″ pause. Make contractions through viii = 35 mm. 9″ pause. Break contraction through viii = 41 mm. 7″ pause.

Then 136 contractions and so on.

10.11. The effect is pushed to almost complete extinction of response from the root ix, and the make contraction from the viii = 32 mm., the break contraction = 36 mm. (Fig. 15).

10.17. The tracing shews the response from ix is irregular and at best hardly perceptible. The response from viii has improved.

10.20. The tracing shews that the response from ix has practically failed. Response from viii make contraction = 40 mm. Break contraction = 46 mm. There is no sluggishness of return of the relaxation line to the base line, (Fig. 15) as was marked at one time (10.11 for instance, Fig. 15).

Compare also the results seen in Fig. 12, Pl. XXIII.

Thus it seems that the fatigue produced by excitation of one of the motor roots of a muscle may affect, *i.e.* slightly diminish the response obtainable from the other motor root. It will be urged that escape of the exciting current from the one root to the other produced the effect. But the fact that the same current which was applied to the "fatiguing" root (ix) did not when applied to vii root, which like the ix also meets the "test" root (viii), escape on to the "test" root, is against its escape on to the "test" root when applied to the "fatiguing" root. And other facts militate against an explanation by escape. If the "fatiguing" root be small and supply a smaller share than usual of the muscle, as evidenced by its yielding from the first a relatively small contraction, the fatigue effect communicated to the "test" contractions may be very slight or apparently wanting; and the converse holds good when the "fatiguing" root is unusually large. This is contrary to what might be expected on an explanation by escape of current, for with the smaller root the tendency for local conditions of stimulation to spread would be greater than with the larger root. Again, in the experiment the extreme diminution of the response elicitable through the "fatiguing" root is due partly to intramuscular fatigue, but partly to changes in the nerve itself at the region affected by the stimulating currents, so that after a while (*e.g.* ten minutes) the intramuscular fatigue is apparently not increased further by the continued excitation of the root, but even diminishes; in the nerve-root to which the stimulating currents are still applied (the "fatiguing" root) the changes are all the while progressing, at least not retrogressing. If the "test" root is affected by the currents applied to the "fatiguing" root then the response obtainable from the "test" root will still continue to suffer diminution, at least will not increase; if on the other hand the "test" response is really influenced by the condition of the muscle-fibres in the fatigued part of the muscle the test response may at this stage not suffer diminution, or may actually improve. In the experiments, as shewn in that quoted above, improvement of the "test" response in the later stage of the experiment does as a matter of fact regularly occur.

The record of contraction has sometimes been taken isometrically, sometimes isotonically; the muscle employed has sometimes been the tibialis posticus, generally the gastrocnemius; in some the "fatiguing" root has been viii, the "test" root ix; generally ix has been the "fatiguing" root: the character of the result has not been essentially altered by these modifications. A condition which does more modify the result is the maintenance or removal of the circulation. When instituted on an excised muscle the degree to which fatigue produced through the "fatiguing" root influences the response obtainable from the test root is more marked, the influence becomes apparent earlier and persists longer. Fig. 14, Pl. XXI. gives an example. If therefore peripheral fatigue be due, as some facts render probable, to genesis by the active material within the muscle fibre of a fatigue substance or substances, potent chiefly upon the motor end plate, the substance or substances in question do appear to be fairly rapidly diffusible from one part of the muscle to another, and to pass quickly through the sarcolemmal sheaths so as to infect adjacent tubules.

The experiments appear to shew that Panizza and Kronenberg were broadly right in supposing that if fatigue be produced in a muscle by excitation of one motor root to it, the muscle will remain still largely unfatigued for excitation by another motor root to it. Yet that to effect this is a main office of the plexal arrangement is hardly likely, because muscular action pushed to the extent of producing great peripheral fatigue, is not of frequent occurrence under natural conditions, central fatigue intervening before the peripheral can occur[1]. Further

[1] Waller. *Brain*, 1891, p. 179.

although the above test experiments prove as I think that the two innervations may be considered, broadly speaking, independent one of another, yet that seems almost the necessary accompaniment of the fact that Kühne, Krause, Eckhardt and others fail to find in muscles innervated by more than one nerve root, that any individual fibre is innervated by more than one of the motor roots to the muscle.

Regarding the physiological meaning of a limb-plexus this much indeed is clear, that by its instrumentality nerve-fibres passing through a number of spinal roots from an extended line of origin in the cord are sorted and collected in such a way that all those destined for one particular muscular organ, *e.g.* the supinator mass of the forearm, the mass of flexors of the ankle-joint, finally exist gathered together in one and the same nerve-trunk. And, to judge from Krause's dissections, any such physiological significance as this if allowed to the constitution of the main cords of the plexus must be extended to such nerves as the median, popliteal, and peroneal. That is to say, judging from Krause, the process of sorting is not completed in the proximal part of the plexus but involves a considerable length of the nerve-trunks. He enquired "ob es nicht möglich sei die anatomische Präparation so zu verfeinern dass man mit dem Messer die einzelnen Faserbündel von den Wurzeln des Plexus brachialis bis zu ihren peripherischen Enden verfolgen könne. Hierzu wurde aus der oben angeführten Gründen die obere Extremität des Menschen gewählt, und die Anwendung chemischer Methoden versucht. Auf diesem Wege ergab sich ein unerwarteter Aufschluss, wie eigentlich die sogenannten Nervenstämme beschaffen sind. Die Nn. medianus, ulnaris, radialis &c. wurden in ihre constituirenden Faserbündel zerlegt, u. nachgewiesen, dass sie selbst richtiger Plexus genannt zu werden verdienen. Die complicirte Structur des N. medianus geht aus Taf. III. sodeutlich hervor, dass eine weitere Beschreibung unnöthig erscheint." Krause abandoned dissection as incapable of answering the question "wo nämlich die Faserbündel der einzelnen Rückenmarksnervenwurzeln an der Peripherie endigen. Die Verhältnisse sind zu complicirt, wie ein Blicke auf die Verflechtungen der auseinander gewissten feinsten Bündel des N. medianus lehrt. Dasselbe gilt wie weiter ausgedehnte Untersuchungen lehrten für die Nn. radialis u. ulnaris." In this conclusion Krause only endorses the prior experience of Morton, Meckel and Swan. Against the conclusion stands however the experience of Walsh (*American Journ. of Med. Sciences, Oct.* 1877, p. 397). And it is difficult to understand if the arrangement be so complex as Krause describes the possibility of such tracing of nerve-bundles along main trunks as was actually accomplished by Herringham.

It is clear that through the plexus definite aggregations of nerve-fibres for definite natural groups of motile and sensitive parts are structurally combined, but the nerve trunks of adjacent somites fuse when the other elements of the somites fuse, and the nerve plexuses may be only one more indication that in the limbs adjacent somites commingle more than do adjacent somites in other portions of the body. The combination of nerve trunks in the plexuses would therefore be but the outcome of the anatomical conditions of the parts. The attribution to them of this anatomical significance does not at all deny a physiological element to their ontogeny. I would be the last to deny a physiological moment in the structural development of the limb.

From the anatomical side, two views of the formation of the limb plexuses are possible. Gegenbaur, Fürbringer, Davidoff and Rosenberg consider the formation of a plexus to be best explicable as the result of shifting of the position of the limb along the spinal axis. As the limb shifts it retains its own nerve-roots and comes into connection with others. In that way the long nervus collector of the skates and ganoids is believed to epitomise the steps of backward travel by the pelvic girdle. But Dohrn and Wiedersheim hold that the Selachian fin originated in the meeting of a number of primitive rays and that as the fin became narrowed at its attached base the spinal nerves proper to it passing through the constricted base came to be more or less fused together.

I here touch upon this question of the ontogeny of the limb plexuses because it bears on the further question of whether a physiological or functional significance as well as an anatomical is to be attached to the distribution of the anterior nerve-roots entering the limbs.

With the anterior spinal roots the case is different from that of the nerve-cords of a plexus. To the former a morphological meaning cannot be refused; for the latter a morphological meaning may be less clear, and, as mentioned above, some writers have denied it. But the belief that a physiological meaning is to be attached to the formation of nerve-cords by the roots of a plexus, and that by that means the various muscles which are known to act together in certain movements are brought together under the dominion of one nerve-root, presupposes a meaning physiological as well as anatomical attaching to the motor distribution of the fibres of the individual spinal nerve-roots themselves. It presupposes and implies that the aggregation of fibres in an anterior spinal root represents some definite coordinated movement of the limb. This idea has been in the ascendant of recent years owing to the conclusions drawn by Ferrier and Yeo from their well-known experiments on the nerve-roots of the monkey. In reference to their results Ferrier and Yeo write, "It will be seen that the movements which result from stimulation of the individual roots of the brachial and crural plexuses are not mere contractions more or less strong of various muscles but a highly coordinated functional synergy in each case, as Remak has supposed." The validity of this conclusion it is a little difficult to test. The mere superficial resemblance of the position assumed by the limb on the excitation of one of its spinal nerves to one of the manifold positions assumed by it in the normal activity of the body appears a somewhat slender basis for the argument. The hind limbs of a frog when it tries to climb the side of the bell jar which confines it assume an attitude of extreme extension with at least an outward semblance of their position during a strychnic cramp or under excitation of the viiith spinal root, but is it permissible from that resemblance to argue that excitation of the viiith spinal root produces really a well coordinated movement of the limb?

Myself I have not been struck by a resemblance between the movement produced by excitation of the subthoracic roots and the coordinated movements of life. If it be urged that in order to obtain the resemblance the excitation employed must be strong, so as to bring into full action every component of the complex entity of the root; when I have done so, the resulting movement has seemed to me, especially in the case of the 6th root, like a strychnia cramp rather than like a movement in coordinate adjustment. If, on the other hand, it be urged that minimal excitation must be used, I have not been able to obtain by that means any more obvious relation to a coordinate movement. For instance, excitation which is just efficient often induces through the 9th root abduction of the tail together with flexion of the digits and the hallux. Extremely feeble excitation of the 8th sometimes produces flexion of the minimus and hallux without movement of the intervening digits, sometimes flexion of the 3rd and 4th digits without the other three, very frequently pursing of the anus together with opposition and flexion of the hallux. These combinations strike the observer at once as bizarre if not grotesque, and, I would maintain, give little suggestion that a highly coordinated functional synergy is brought into play.

When several of the motor spinal roots belonging to a limb-plexus are cut through, the immediate effect upon movements executed by the limb is expressive of helplessness and weakness of movement rather than of incoordinate movement. For instance:

Macacus Rhesus, young ♂. The 8th cervical and the 1st and 2nd thoracic motor roots divided on the right side in the spinal canal; two hours later the animal keeps the forearm flexed, and the wrist midway between prone and supine positions. He does not often attempt to use the limb, apparently preferring to use the left. Occasionally he is induced to use it, and it is seen that the forearm can be flexed well, the hand well shut, and he takes my finger in his own with a fair grip; there is no obvious hesitancy or tremulancy of movement, and the fingers seize accurately the thing (*e.g.* my finger, the ledge of the table, the side of a shelf, a loop of string), which apparently he intended them to take. The grasp is however much weaker than that of the other hand, and does not appear to be executed quite so quickly, nor in quite the same manner, although in what the latter difference consists is not clear.

Macacus Rhesus ♀. The 4th, 5th, 6th and 8th cervical roots and the 1st, 2nd and 3rd thoracic roots of the right side divided intraspinally. Three hours later the following note was made as to movements of the right arm.

The limb is allowed to hang vertically at the shoulder joint. It cannot be raised at that joint, as for instance for the forward stroke swimming or for reaching an object above, nor can it be brought forward over the front of the chest. It can be drawn backward at the shoulder-joint and when it has been raised it can be brought down with considerable force as in the backward movement of the swimming stroke. There is some power of flexion at the elbow, but it is slight. The forearm is kept extended. As the arm droops (the animal sitting down) the hand is on the floor, lying with the palmar surface upward, but the position of the wrist is pronation. There is some power of flexion at the wrist, but apparently no power for extension at the wrist. There is some power of grip in the hand, as tested by allowing the animal to hold my finger. There is apparently great disinclination to attempt a movement with the limb, but no incoordination of the movements undertaken, although the movements are feeble and appear somewhat slow.

Macacus Rhesus ♀. The motor roots of the 3rd, 4th, 5th, 7th and 8th cervical and of the 1st and 2nd thoracic nerves divided on the right side. Two hours later the following note was made:

As the animal is quietly seated, the head is turned somewhat away from the right side, and there is prominence of the sterno-mastoid muscle; the right shoulder is low; the forearm is kept at about a right angle with the upper arm, the wrist is placed with the radial edge upward, the hand midway between prone and supine, the fingers and thumb are semiflexed. No extension of the shoulder is seen to occur. When I extend the forearm it can be brought back to semiflexion but very slightly beyond semiflexion (i.e. forearm at 90° to upper arm). In doing so biceps and supinator longus can be felt contracting. Flexion of hand not seen to take place. The grasp is wholly lost. When the body is inverted as occurs when the animal comes down from roof of cage the right arm hangs downward, and an attempt to raise it, *i.e.* to bring it up to horizontal with head, or to bring it to side, fails. Apparently the hanging limb can not be brought to side of trunk. In the attempts and failures and in other movements carried out successfully there is observed no want of coordination, as evidenced by misdirection, or by apparently purposeless or jerked or indirect motion. Feebleness of movement and unwillingness to attempt movement seemed obvious enough but not incoordination.

Macacus Rhesus. The 4th, 5th, 6th and 7th cervical ventral roots of the right side, and the highest four thoracic roots of that side divided inside the spinal canal. Three hours later the following note was written. "The arm droops at the shoulder, but can be raised to some extent. At the elbow three-quarter extension is maintained. The forearm can be flexed to some extent, the radial edge of the wrist being kept uppermost in so doing, and the hand thus being midway between prone and supine. A certain amount of grasp of the hand is retained; my finger is taken with a feeble hold but without clumsiness."

Macacus Rhesus ♀, young. The 5th, 6th, 7th and 8th cervical and the 1st and the 3rd, 4th, 5th and 6th thoracic roots severed on the right side. Note written three hours later. "The right arm droops. The hand is occasionally closed, the fingers and thumb folding together in a slow manner but without any sign of want of coordination in their synchronous movement; the closure is not a tight one: my finger is merely loosely held. Slight flexion at the wrist certainly accompanied the movement once, but was not noticed on the other occasions. No other movements observed within the limb."

I preferred to examine this point by experiments on the upper limb because I feared being misled in observations on the lower limb by the impressions already received from my own experiments on its plexus. Observations of the kind I have however also made on the lower limb.

Macacus Rhesus. The 6th and 9th subthoracic roots divided on the right side within the spinal canal. One hour later, no obvious clumsiness of movement but great reluctance to move it. Grasp by the right foot is feeble, *e.g.* when the foot is grasping the side of the cage the foot can be quite easily loosened from the cage by pulling on it, whereas it is difficult to loosen the grasp taken by the left foot. There is also some difficulty obvious in rising from the squatting posture, the body seems to be lifted chiefly by the left leg.

Three months later (82 days); no clumsiness or incoordination in movement of limb noted. No obvious reluctance to use the limb. The grasp however of the right foot is still feeble, as feeble as at first: there is still the appearance as if in rising from the sitting posture the left limb was the chief power. I believe this appearance not to have been present in the animal before the operation, for it had been in the laboratory under observation some time previous to use, and further because a very similar appearance was seen in a monkey in which the 7th, 8th and 10th roots had been divided on the right side. The tail in that animal deviated to the left side (in consequence of the root lesion), and as the tail lay under the left ham it was noticeable that in lifting the body from the sitting position the left ham had sometimes been lifted from the tail lying under it before the right ham was free of the board of the shelf on which the animal was squatting.

In other experiments in which the 6th and 7th roots, the 8th root alone, the 3rd and 4th, 6th and 7th, the 4th, 5th, 7th and 8th, the 6th, 8th, 9th and 10th were divided, there was no clear evidence of incoordination of movement as a result immediate or remote. Movement was rendered somewhat slow at first and was enfeebled. The evidence was rather that of a weakened condition of many movements; only when the number of consecutive roots was more than two there appeared a certain limitation of the range of movement by complete loss in some particular direction. The helplessness, at first in some cases very apparent, rapidly diminished up to a certain point. The diminution seemed to be largely due to the overcoming in course of time of an unwillingness to attempt movements with the injured limb. Thus the animal with division of lowest cervical and the upper two dorsal roots of the right side was at first never seen to attempt to use its right arm to climb to its shelf and could not be induced to do so, but directly the left arm was bandaged, on climbing to its seat it used the right and did not misdirect the movements of it. Two months after the lesion the same animal returned to its shelf sometimes voluntarily using the left side of the cage, sometimes the right, the right arm being used in going up by the right-hand way, the left arm by the left-hand way. Again, the animal with severance of the 7th, 8th and 10th roots on the right side was unwilling at first to climb the side of the cage or to rise from the squatting posture, but could if need be do both; later it displayed no unwillingness to do either, and ran freely about the cage, to casual observation not obviously abnormal.

That the loss of some particular coordinated movement results from the severance of one of the motor roots to the limb plexus, I have been unable to detect, and seen no evidence to support. But it might be expected to do so on the view that the compound movement obtained by excitation of a whole nerve-root is a well coordinated one depending on the action of a group of muscles in synergic combination. I gather from the experiments just mentioned and from similar ones on the frog that the execution of a coordinated movement is still possible when one motor root only of the plexus remains open as a channel from the cord; that equal excitation of all the fibres of one efferent root produces a coordinated movement, still less a well coordinated one, there is it seems to me no evidence to shew.

And there is another objection to the view. When it is remembered that excitation of small bundles taken separately from the fibres of the anterior root give movements that do not obviously differ from one another in character, although the groups taken be of natural composition, that is to say, composed of fibres arising together at the line of exit of the motor root from the cord, it is clear that by the grouping of the fibres in their outflow only a comparatively few of the many coordinated movements of the limb can possibly be expressed, and in for instance the frog where only three motor roots enter the hind limb, the number becomes so limited that it seems a natural question to ask why when so much of the coordination of movement of the limb is left unexpressed in the simple anatomical terms of groups of fibres forming spinal anterior roots, any at all of the coordination should be represented in that way? Is the special coordination of the movements discoverable to us in that kind of way at all? Is it not rather associated with arrangements inside the cord largely incapable of representation by anatomical grouping fettered as that grouping must be by old standing relations of posterior and anterior, superior and inferior, medial and lateral, heritages from ancestral segmentation?

The following observations bear I think on this question. One of the filaments of which the ventral root of the 8th or 9th subthoracic spinal nerve is naturally composed is laid bare in the spinal canal, is isolated, divided across, and after division its long peripheral portion (several centimeters in length) lifted up clear of the other rootlets, laid upon the sheathed electrodes and then stimulated by weak tetanising currents of just above minimal efficiency. There results closure of the foot by flexion of all the digits and adduction of the minimus and hallux with some opposition of the latter, a movement similar to that following excitation of the whole ventral root in its entirety; it is true the movement although similar is not so forcible. If on the other hand the central end of a filament of the dorsal (posterior) root of the 8th or 9th spinal nerve be similarly excited a movement in the foot is produced which usually consists in simple adduction and opposition of the hallux with some flexion of it, but with no movement in the other digits at all. If instead of a filament of the dorsal (posterior) root in question the whole root be taken a similar result is obtained, and with a weaker current. A most intimate commingling of the efferent fibres to the intrinsic muscles of the foot must therefore exist along their line of outflow from the cord. Fibres for the most posterior and anterior individual muscles must coexist in the same root-bundles side by side. Isolated action of a single digit, *e.g.* hallux, is thus difficult or impossible to obtain by direct excitation of competent strength applied to efferent nerve roots, isolation by anatomical means of the filaments in the motor roots not leading to isolation of sets of efferent fibres for definite functional movements. But isolated action of a single digit, *e.g.* hallux, may be readily obtained by appropriate excitation of afferent roots of the cord, even when excited in such considerable bulk as for instance the entire dorsal root of a large spinal nerve like the 8th or 7th subthoracic of Macacus. Moreover a not inconsiderable range of strength of stimulus applied to the central end of the dorsal (afferent) division of the spinal root will evoke simply flexion and opposition of the hallux without movement of the other digits, whereas it is somewhat difficult to find for any motor root or root-filament a particular pitch of excitation which will cause movement of one digit without contemporary movement of others; sometimes in the efferent roots I have not succeeded in finding any strength of stimulus which will give movement of one digit without movement of the others as well, but it is generally possible with patience to do so, and sometimes the hallux is the digit which is earliest to reply on gradually bringing the excitation from below minimal up to the minimal point. The inference from the experiments I take to be that the spinal mechanism for individual movement of any such one part of the limb as a single digit is so distributed in space that the anatomical arrangement of the efferent fibres debouching from it into the spinal roots does not allow in any one root-filament of a perfect representation of the one movement, but only of an imperfect representation of several adjacent local movements though not for each equally imperfect.

Again, by the method of minimal excitation I have failed to find evidence that the movement produced by a single efferent root is in nature a truly coordinate one. In examining the point it seemed that no more favorable field for test could be employed than the foot or hand and the movements of the digits. As has already been adverted to the effect of minimal excitation of such efferent roots as the 6th, 7th, 8th, or 9th subthoracic has not always in my hands given quite similar results. Frequently such quaint and bizarre movements as flexion of hallux and minimus together, or of only third and fourth digits together or of index alone, etc., have been the results of the minimal excitation, so that although movements which do not bear on the face of them any obvious incongruity or want of co-adaptation have not been infrequent, such for instance as flexion of hallux and all the digits or of hallux and index together, I am less disposed to consider these latter as truly coordinate and the numerous others as accidental errors of experiment, than to believe that the apparently coordinate movements were really no more so than the obviously incoordinate, and merely appeared coordinate because one has only superficial means of judging of coordination of movement even in such a comparatively favourable field as the delicately mobile foot of the macacque. It is true that it may be objected that the method of minimal excitation is a fallacious guide, and that it yields at best an imperfect picture of the capabilities of the nerve to which it is applied; yet it affords a useful idea of the main distribution of the trunk and helps to differentiate the main from the subsidiary. Also it may be objected that in the movements obtained at least flexion went with flexion, extension with extension, that is to say, that no movement was observed such as flexion of the index together with extension and abduction of the hallux. That is true, but is as explicable by the segmental and purely anatomical view of the composition of the roots as by the view which attaches to them a functional constitution, because as shewn on page 748 *infra*, circumstances of purely segmental and morphological moment would place together the flexors of joints equally far down the axis of the limb and would place the extensors of so situated joints together, and because the levels of greatest spinal representation of, or of greatest spinal out-flow to, the flexors and extensors would not fall within the same segment of the cord. Nor should I, had it happened, have considered that extension of certain digits contemporaneously with flexion of others necessarily indicated want of coordination. Flexion and adduction of the hallux with extension of the other digits especially at the metatarsophalangeal joints, I have frequently seen occur as a spinal reflex movement in the foot of Macacus rhesus just as one frequently sees it occur on excitation of the leg area of the hemispheral cortex[1]. Because I was well acquainted with the movement as a spinal reflex I looked for it with especial attention when exciting the individual efferent roots of Macacus or the component filaments of them, and can affirm that I never saw it occur under those conditions once, although the number of separate excitations made must run into several hundreds.

Further, in the variability of the relation of any particular ventral root to any particular muscle the conception of the root as representing a highly coordinated functional synergy encounters difficulties almost insuperable. In the same species the sixth subthoracic efferent root occasionally gives extension of the knee, although in most individuals flexion, again, in one individual folding of a digit, in another straightening. And between these extreme types of difference there are intermediate types each of which must exhibit according to the above view a coordinate synergy peculiar to the individual.

If the collection of fibres in each anterior root is really the representation of a highly coordinate functional synergy it is hard to conceive why the sacrococcygeal muscles in both rhesus and cat are supplied from the 8th and 9th roots, so that in the movement belonging to the 8th root there is associated with flexion at the knee, extension at the ankle and folding of the toes, a strong lateral deviation of the tail, and a smart tightening and pursing of the anus. Or in the movement of the 9th root why there should be pursing of the anus accompanying flexion of the digits and the hallux. Why should constriction of the vagina be inseparable from closure of the anus; why the hallux opposed at the same time as the urinary bladder evacuated? These affinities of action, strange to explain on the theory of the synergetic origin of the motor root, appear natural and in accordance with expectation when viewed from a morphological stand-point.

The fact that the same ventral root often innervates opposing muscles does not necessarily offer any contradiction to the statement that the movement produced by excitation of the root represents a highly coordinated functional synergy because as is well known opponent muscles frequently act in concert. Indeed the fact that the same root is often motor to antagonistic muscles although pointed to by Eckhardt as adverse to the functional view of the constitution of the root, may equally well or even more fittingly be mentioned as an argument in its favour. It is for that reason a point demanding some examination here.

[1] Cf. also Beevor and Horsley, *Phil. Trans.* 1888, B. p. 205.

Duchenne[1] and Rieger[2] have maintained that in all voluntary movements two sets of muscles which exercise antagonistic action are thrown simultaneously into contraction. Pettigrew[3] has advanced somewhat the same view, and indeed Winslow[4] seems to have been its earliest exponent. Beaunis[5] has however concluded from experimental observations that in some movements one set only of the antagonistics contracts, the other remaining inactive. Brücke[6] and more recently Demeny[7], and Beevor[8] have shewn that in certain natural movements of the human body one member only of the antagonistic couple is employed. If antagonistic muscles are sometimes coordinated in their action in such a way that during movement one element of the couple is passive while the other is contracting, it is clear that for carrying out such examples of coordination the anterior spinal root as a whole is not a suitable instrument. Not even the small natural bundles composing the root can where, as is the rule, each bundle is like the root itself distributed to antagonistics, be as a whole concerned or employed. If the natural filaments of the anterior root of the 7th subthoracic be taken according to their serial position in ten small bundles and be each excited with a current sufficiently strong to stimulate all its fibres equally, each and every bundle gives contraction of both flexors and extensors of the ankle joint. So that neither by the root itself nor any one of these its root bundles taken in its entirety can a coordinate movement employing only the precrural or only the postcrural muscle group be carried out. The same is true of flexion and extension at the wrist and of the 8th cervical root. I have taken some further observations bearing on this point.

Selection was made of a pure ginglymus joint acted upon by a strictly antagonistic muscular couple, the antagonistic couple being innervated by nerve-roots which each supplied both of the two components of the couple. A joint which fulfils these conditions is the tarso-crural of the frog with its precrural and postcrural sets of muscles, and its motor-roots, namely, those of the 8th and 9th spinal nerves. Each of the roots supplies both the precrural and postcrural muscle-groups (Fig. 3.

1 *Physiologie des movements*, 1867, p. 766.

2 *Archiv f. Psychiatrie*, XIII.

3 *Animal Locomotion*, 1874.

4 *An anatomical exposition of the structure of the Human Body.* 1749.

5 *Travaux du Laborat. de Physiol. de Nancy*, 1884.

6 *Wiener Sitzungsberichte d. k. k. Acad.* 1877.

7 *Archiv de Physiol. normal et path.* 1890. p. 747.

8 *Brain.* 1891. p. 54.

Pl. XXIII.). After the brain had been destroyed the hind limb was fixed and as regards the hip and knee its joints absolutely immobilised by metal clamps or by rivets passed through or holding the femur and the os cruris; the foot was removed; the tendo achillis or the tendon of the tibialis posticus was attached to a myograph lever in the usual way; in like manner the lower tendon of the tibialis anticus or of the peroneus or occasionally the lower end of the calcaneo-astragalus was attached to a second lever in the myograph. The levers were of similar length and were set to write approximately in the same meridian of the recording cylinder, sometimes they were so set as to write in the same sense, sometimes in opposite senses[1]. The levers were so arranged that the muscles attached to them when at rest were under a stretch just sufficient to restore the muscles to the length they possessed when the ankle joint was semi-extended before section of the tendons. When the recording surface had been set in motion a reflex action was induced by touching the skin of the back or perineum, or by placing on the skin a square millimeter of blotting-paper moistened with acidulated water. Tracings were then obtained of the contractions of the antagonistic muscles during their coordinated action. The records shewed that frequently the antagonistic muscles were during the greater part of the movement in contemporaneous activity, though not mutually active to equal extent in the various phases of the movement. The extent of their contraction varied from moment to moment both relatively and absolutely, indeed it was quite frequent for the movement to begin and especially frequent for it to end with isolated activity of one member only of the antagonistic pair (Figs. 2, 5 and 11). It is obvious therefore that in these instances of coordinate movement the mutual behaviour of the antagonistic muscles did not answer to that occurring under competent excitation of any single ventral root. A comparison of the graphic records in the two cases merely renders the more obvious the profound difference existing between the two movements (cf. Figs. 2, 3, 5, 11, Pl. XXIII.). Not infrequently in movements of small amplitude and short duration one set of the antagonistic pair is alone measurably thrown into contraction (Fig. 9). Inasmuch as each nerve-root that supplies the one set innervates the antagonistic as well, it is here obvious that the coordinate natural movement is again widely and fundamentally different from any which could be stimulated by competent excitation of either spinal efferent root.

[1] Occasionally instead of a time marker, vibrating styles were used.

Frequently the observations discovered *accurately alternating* contraction of the two sets of muscles acting on the joint (Figs. 5, 11, Pl. XXIII.), so that had the tarsus been still connected with the muscles an alternating flexion and extension of considerable amplitude and force would have resulted at the joint. Such movement one does not unfrequently see when in a frog tied to the frog plate but otherwise untouched a piece of moistened paper is laid on the skin near the anus; one sees such movements also though not so frequently in frogs deprived of the cerebral hemispheres. I endeavoured to record such movements while all the muscular attachments were still left untouched (Fig. 4), by fastening to the myograph lever a thread passed round the intact tarso-metatarsus, and then after obtaining the record have proceeded at once to register from the separated tendons of the antagonistic group (Fig. 5). In that way one can sometimes obtain an approximate analysis of the previous forward and backward movements of the foot, and the analysis entirely supports the idea that the movement of the foot has been produced by alternating rather than by synchronous contraction of the antagonistic groups. Often the action of the two groups was strictly alternate to the degree that relaxation commenced in one set in the same fiftieth of a second as contraction was entered on by the other (Fig. 8). That for such alternating action neither of the only two ventral spinal roots which could possibly have been concerned, viii and ix, was actually employed as a whole, i.e. as one functional entity, is clear because the roots contain fibres each of them for both sets of antagonistics. Throughout the continuance of these alternating movements the records reveal (cf. Figs. 5, 11, Pl. XXIII.) no period in which the condition of the two groups corresponds with their reciprocal condition on excitation of the anterior spinal roots supplying the leg. That condition is strong action of both precrural and postcrural sets. In order to see the result of excitation of one entire ventral root when the excitation is somewhat more sustained than it is under the mechanical stimulation employed, in order to ensure freedom from escape of stimulating current in such records as shewn in Fig. 3, and yet at the same time to be certain of confining the excitation to the one root alone I used strychnia after cutting all the ventral roots except the one desired. The graphic records shewed a very synchronous action of the two muscle groups quite different from the registers of reciprocal contractions reflexly produced (Fig. 7). In order to have a control to the possible degree to which any mechanical drag of one set of antagonistics might influence the graphic record obtained from the other, although with the limb-bones firmly fastened any such source of error can scarcely arise, the antagonist records were taken sometimes both of them in one and the same direction and sometimes in reversed directions. I also took a few records of the contraction of muscles in the same group instead of in antagonistic groups, in the belief that if as one might suppose they acted synchronously, the degree to which that synchronicity was translated upon the double record would form a gauge to the degree of mechanical isolation of the two muscular records. Fig. 1, Pl. XXIII. shews a record of the synchronous action of the tibialis anticus and peroneus muscles under reflex excitation; both of the muscles are flexors of the ankle joint.

In Macacus movements can be evoked from the hemispheral cortex which demonstrably employ certain only of the fibres of particular nerve-roots, and do not involve other fibres existing in the same nerve-roots. Thus in the commonly combined movements of flexion of hallux into the sole with extension of the other digits there are employed many of the fibres of the 8th, 7th and 6th roots but not, unless movement of the ankle be superinduced, the fibres for the post crural muscles, the peronei or the tibialis anticus in those roots. Yet in this movement both of the antagonistic groups are at the same time in play, for on section of the plantar nerves the flexion of the hallux is replaced by extension, or on section of the peroneal nerve, extension of the small toes is replaced by flexion of them.

Not however in every instance is it possible to *reverse* the "cortical" movement by section of the motor nerve to the preponderant muscle-group. When the movement of advance of the whole upper limb with extension at all its joints is evoked from the cortex, the effect of section of the musculospiral trunk in the axilla is as regards the elbow-joint to simply abolish the extension, not replacing it by flexion. In all of five experiments I have seen this the case.

Example. Macac. rhes. ♀. 8. XII. 91. Chloroform and ether.

1.35 P.M. The musculospiral, median, and ulnar trunks exposed in the right and left axillæ.

1.47 " Parts of "motor" cortex right and left exposed.

2.13 " Secondary coil at 13 cm. Excitation of left hemisphere at a point *a* (about midway between sulc. centralis and the top bend of sulc. precentralis) is giving consistently *advance of shoulder followed by extension of elbow, then extension of wrist and digits.* Excitation is repeated several times with the same result.

2.20 P.M. Same stimulus elicits same reply from α as at 2.13. Then section of right musculospiral trunk.

2.22 „ Same stimulus applied to point α evokes advance of shoulder followed after a pause by *flexion* of digits and the wrist: at elbow no active movement, neither flexion nor extension: the final flexion at the wrist seems to follow decidedly later than did extension of wrist in the sequence obtained prior to cutting the musculo-spiral.

2.25 „ Same result as at 2.22.

2.38 „ Similar movement as obtained at first from α got from a point β in right hemisphere.

2.46 „ Left musculo-spiral cut with similar result on movement evoked from β.

In the extension at the elbow produced by the stimulation of the cortex the extensors only of the antagonistic muscles were being employed, but in the extension of the digits probably both extensors and flexors were together brought into play. The observation of Beevor[1] that in man flexion of the forearm is sometimes performed without the least detectable contraction of the brachial triceps, lends interest to the above result.

There seems a difference between the larger and smaller joints of the limb in respect to associate action of their antagonistic muscles. Certainly in the case of the small joints of the foot and hand the movement produced by excitation of the cortex is most usually not merely cut out but reversed by section of the motor nerve to the preponderant of the antagonistic sets. This is illustrated by the following tabulated list of observations[2].

No. of Expts.	Part moved	Nature of Movement	How evoked	Effect of section of the peripheral nerve-trunk	
				No. of abolitions without "reversal"	No. with "reversal"
7	pollex	flexion with adduction	stim. of "motor" cortex	0	7
9	hallux	flexion with adduction	,,	2	7
3	hallux	extension with abduction	,,	0	3
6	small toes	extension with separation	,,	1	5
8	fingers	flexion	,,	1	7
12	hallux	flexion with adduction	stim. of afferent spinal root	10	2 (each time barely perceptible)

[1] *Brain*, 1891, *loc. cit.*

[2] I hope shortly to publish a more extended series.

I have appended to the list the flexion with adduction of the hallux evoked from the sensory spinal nerve-root because although it to me seems indistinguishable by inspection from the corresponding movement evoked from the cortex, it appears different from the latter when examined by the above experiments. In the movement when produced from the cortex, both sets of the antagonistic pair usually participate; when produced by weak excitation of the afferent sacral roots the extensors do not participate in it to nearly a like extent, *i.e.* one set only of the antagonistic pair is employed.

It might perhaps be urged that this apparent difference between the antagonistic association of muscles about large joints and small indicates a functional character in the arrangement of nerve-fibres of the motor spinal root because it is consonant with the fact that the spatial separation in the cord between the outflows of motor fibres for the flexors and extensors of the small joints is greater than in the case of the large, of the digits for instance than of the knee and elbow. But it must be remembered that the joints of the digits are not merely the smallest, they are also the most distal in the limb, and the larger joints are also the more proximal. The greater overlap of the efferent fibres for the antagonistic muscles of the digits is related to the distal position of the digits. It is a necessary corollary from the constitution of the limb out of a series of rays which are of increasing length as counted from the foremost backwards. But to refer to this morphological arrangement the fact that, under cortical excitation, the association between the antagonistic muscles of the digits is apparently closer than between those of, for instance, the elbow is obviously unwarrantable. That is to say, in the fact that several motor roots each yield extension at the knee with perfect passivity of its flexor muscles while it is questionable whether any can extend the digits with passivity of their flexors, there is no necessary implication that under cortical excitation it will be easier to isolate from one another the activities of the antagonistic muscles of the knee than of the hallux, of the elbow than of the thumb. The cortical difference is more probably related to the extreme fineness and nicety of adjustment of the movements performed by the small joints at the free end of the limb.

The evidence thus obtained does not therefore afford support to the view that the collection of motor fibres in an anterior root represents a highly coordinated functional synergy.

It may be objected that the isolated and alternating activity of antagonistic muscles in coordinated movement does not militate in the argument because it is exceptional rather than the rule. Without venturing to decide to what extent such mode of action is in the limbs exceptional, I must think it is certainly not exceptional in certain situations, for instance in the intercostal spaces where Martin and Hartwell[1] shewed that an alternating action of the internal and external intercostals goes forward in the normal breathing of the dog. But both the internal and external intercostal muscle of the space receive their motor supply from the one same anterior root, namely that belonging to the space they occupy.

In judging of the significance to be attached to the constitution of the motor root another line by which a criterion may possibly be reached lies in the gauging of the degree of mutual dependence or independence, in actions on the one hand undeniably coordinate and on the other hand due to direct stimulation of the motor root, of the long and short muscles of the digits. Among movements easily accessible to experiment those evoked by excitation of the cortex may be taken as irrefutably coordinate, and, somewhat less satisfactory perhaps, the above-described reflex flexion of the hallux into the sole obtained from excitation of an afferent sacral root. Of the latter movement I have already mentioned that by section of the plantar nerves behind the heel it is immediately and absolutely abolished, occasionally a scarcely perceptible movement of extension appearing in its place. Here then the contraction of the short flexor appears altogether unassociated with any contraction on the part of the long flexor. As to the flexion of the hallux given by cortical excitation I have in all of nine experiments on Rhesus found the movement completely abolished by section of the plantar nerves at the heel, so that in these cases the short flexors under cortical stimulation were acting absolutely independently of the long. After section of the plantar nerves it may be by no means easy to evoke from the cortex any flexion of the hallux. Readily excited from the cortex as are the short muscles of the hallux the long flexors seem by no means so readily brought into play. I mention this as bearing on the question of the mutual independence of the two sets in the performance of coordinated movements. To turn now to direct excitation of the motor spinal root; when flexion of the hallux is produced by the 7th, also often by the 6th or 8th subthoracic roots, both short and long flexors[2] participate together in the production of the flexion. And the type of flexion of

[1] This *Journal*, Vol. III. p. 24.

[2] The plural is used because in Macacus the *flex. long. digit.* as well as the *long. hallucis* is an actual flexor of the hallux.

the hallux produced by cortical excitation is not appreciably altered by severance of the 8th or 9th subthoracic root. Here also therefore a difference in character divides the coordinated movement from the movement represented in the spinal root.

The ontogeny of the brachial limb is of course distinct from that of the pelvic limb, the correspondence between the two is similarity not identity. It has been shewn for the pelvic limb that in many individuals the most posterior portion of the outflow of efferent fibres from the cord to the skeletal muscles of the limb, *i.e.* that to the plantar muscles, extends backward into the ventral root of the 9th subthoracic nerve. That 9th root, the hindmost to the limb muscles, supplies of the intrinsic muscles of the limb almost always the plantar only. In the brachial limb just as in the pelvic the efferent outflow to the small muscles of the distal region of the limb, *i.e.* to the palmar muscles, occupies the posterior end of the entire outflow of efferent fibres to the limb, extending into the 2nd thoracic root. In the case of the brachial limb however, not as in the pelvic, the hindmost motor root contains efferent fibres to the long flexor muscles of the digits as well as to the short. Therefore, in the arm the last motor root innervates the short and the long flexors of the digits together, in the leg the last motor root innervates the short flexors of the digits and never the long flexors. If each individual motor root is a construction synthesised by function and represents some "highly coordinated functional synergy," then in the arm the functional association between the long and short flexor muscles of the digits is closer than between the corresponding muscles in the leg. But experimental analysis by cortical excitation affords no sort of confirmation for this inference; action of the short flexor of the pollex apart from action of the long flexor is just as, perhaps more, easily obtained than is the similarly isolated action of the short flexor of the hallux. On the other hand to the view of the constitution and significance of the motor root which I am advocating in this paper the above arrangement opposes no obstacle whatever; on that view a general, not a particular, resemblance is to be expected between the plexus-roots of the two limbs.

Further, if the collection of efferent fibres in each root represents a well coordinated movement, depending on the action of a group of muscles in synergic combination, it might be expected that the combination would as an individual entity be somewhat readily called into play reflexly through the central end of the afferent root of the same segmental nerve. This expectation is not borne out by experiment so far as I have seen. On excitation of the central end of the afferent root, say that of the 8th subthoracic root, part only of the muscular region supplied by the ventral root is at first involved in the resulting reflex movement, and there is no accurate simulation of the movement given by equal excitation of all the fibres of the motor root, until much stronger stimuli are used than those which lie near minimal for the reflex irritability. Ultimately when at last the movement produced does appear to embrace all the muscular region supplied by the particular efferent root in question it is accompanied by other movements which evidence that other efferent roots than the one corresponding to the afferent root stimulated are in action either partially or completely. The following experiment affords example of this.

Macacus rhesus, ♂. Ether and chloroform. January 27, 1891. Excitation of central end of afferent root of 9th left sub-thoracic nerve by rapid series of induced currents from the Du Bois inductorium. One pint Dan. in primary.

11.10 A.M. Secondary coil at 45 cm. on the scale (current perceptible to tongue at 21 cm.), excitation gives slight pouting of lower half of anus.

at 33 cm. pouting of anus more marked, root of tail is drawn to the left side slightly.

at 30·5 ,, outer hamstring muscles contract as well as the above; the foot is slightly everted.

at 26 ,, adduction and flexion of the hallux in addition to the above.

at 22 ,, of the digits as well.

at 19 ,, adduction of opposite thigh as well.

(A very interesting point of repeated occurrence in experiments of which the above is an example is the high resistance evidenced as existent between right and left halves of the cord, and the fact that when the excitation is finally pushed sufficiently to cross the median line of the cord in this region it embouches thus early into mechanisms for the anus and the adductor muscles of the opposite thigh. Cf. supra p. 675.)

11.30. Excitation with secondary at 44 cm.—35 cm. of central end of 8th sub-thoracic root gives flexion and adduction of hallux and no other movement in foot.

11.33. Central end of 7th gives same as of 8th, secondary coil lying between 47 cm. and 38 cm.

11.35. Central end of 6th root gives same as of 7th, secondary lying between 45 cm. and 34 cm.

11.45. Minimal excitation of the anterior root of the 9th gives closure of anus with adduction and flexion of hallux and minimus (secondary at 76 cm.). The anus, hallux, and minimus are more easily thrown into action than the three remaining digits, but the latter are included when secondary is pushed to 75 cm.

11.47. In exciting the anterior root of the 8th, I am unable to find a pitch of excitation capable of isolating the movements of the anus, hallux and minimus from one another. By excitation of the central end of the posterior root it has been easy to obtain an isolated movement of the hallux.

11.58. Excitation of central end of posterior root of 8th nerve of right side gives a movement (flexion and adduction) of the hallux without other digits, when secondary coil ranges between 32 cm. and 27 cm.

12.6. Minimal excitation of distal end of a filament from middle of the anterior root of 8th right-hand nerve gives flexion of hallux and all digits (secondary at 51).

It seems that it is not easy to evoke reflexly by excitation of the dorsal (afferent) root of a spinal nerve that combined movement which excitation of the ventral (efferent) root of the nerve readily evokes. That is to say, if the combined movement given by the ventral (motor) root does really represent a functional coordination it must nevertheless be admitted that the spinal mechanism connected with it, which should presumably lie not far distant from the root that is its instrument, is not of easy approach by the local channel of even its own afferent root.

For this to be the case seems to indicate that studied from a functional aspect the spinal mechanisms subserving movements in a highly developed mammalian limb retain scarcely more than vestiges of the segmentation one supposes marked them in the early phases of the genetic history of the limb,—that in its development adaptation to new conditions increasing its complexity has diminished the individuality of the segments and welded them very thoroughly together. In regard to this point I have not obtained good experimental evidence that the reflex muscular mechanisms of the limb are separated from one another into more or less obviously segmental divisions, as one might expect did the efferent outflow from each segment of the cord in this region represent a functional coordinated synergic combination. There seemed in my experiments to be no demonstrable barrier to the passage of impulses from one segment into another; afferent impulses poured into one segment could evoke efferent impulses as easily from the adjacent segments as from the actual segment into which they were themselves thrown. No resistance to nervous irradiation from one segment into the adjoining appeared in many cases to be demonstrable. For instance:

Macacus rhesus, ♀. 5. iii. 91.

4.32 P.M. Central end of dorsal root of 7th sub-thoracic nerve, gives on excitation with 2nd coil at 43 cm., flexion of hallux. No contraction of anus.

4.34. Central end of dorsal root of 8th sub-thoracic nerve gives on excitation with coil at 39 cm. weak flexion of hallux. Slight contraction of anus.

4.35. Ventral root of 7th nerve cut.

4.36. Central end of dorsal root of 7th gives flexion of hallux at 43·5 cm. without contraction of anus.

4.38. Central end of 7th gives flexion of hallux at 44 cm., without contraction of anus.

4.40. Central end of 8th gives flexion of hallux at 39·5 cm., with contraction of anus.

This monkey was found by further excitations to possess a plexus of the *postfixed* class, hence the reflex obtained from the central end of the dorsal root of the 7th must have been chiefly carried out through 8th and 9th after section of its own ventral root, and it was obtained as easily as when its own ventral root was intact.

The solidarity of the essentially segmented cord must here be extraordinarily complete.

On the other hand between the efferent fibres contained in one and the same spinal root there may intervene a relatively high nervous resistance. Between components of one and the same spinal segment a considerable physiological barrier may be interposed. I was much struck with this possibility during some experiments on the bladder. Although the 9th subthoracic nerve contains efferent fibres for the urinary bladder it is not easy to obtain a reflex effect upon that organ by excitation of the central end of the afferent division of the 9th nerve root. Excitation of the afferent division of the root readily gives a reflex in the anal and limb musculature, but not until the excitation far exceeds the minimal for those reflexes is any effect upon the bladder obtained. By stimulation of the central end of even the whole sciatic trunk it is not easy to elicit reflex contraction in the bladder. The 4th lumbar root gives efferent fibres to the bladder, but electric currents applied to the afferent division of the root in order to produce reflex contraction require to be so strong as, in my hands at least, to have left it uncertain whether the apparent reflex were not really referable to escape of current on to the efferent division of the root[1]. A great difference between the bladder and the anus exists in this respect. The bladder appears to be cut off from the skeletal limb muscles by a high intraspinal resistance; between the anal muscles and the limb muscles no such high barrier of resistance seems to be placed. It is perhaps to be considered a resistance interposed between the skeletal and the visceral elements of the spinal segment. In regions other than the lumbar if a spinal root be selected the efferent division of which contains both fibres for skeletal muscle and sympathetic fibres, excitation of the proximal end of a branch of the somatic division readily calls into play the somatic efferent division, but not readily the visceral efferent division (sympathetic). Thus the 2nd thoracic spinal nerve of Macacus rhesus consists on the one hand of a sensori-motor somatic portion that divides into a sensori-motor branch to the limb and a sensori-motor branch to the 2nd intercostal space; and on the other hand of an efferent sympathetic part that contains pupillo-dilator, pilo-motor, vaso-constrictor and other fibres. On exciting the central end of the branch to the 2nd intercostal space reflex movement in the hand is obtained by stimuli of moderate intensity (induced currents just perceptible to the tongue); yet no effect on the pupil or the hair is obtained even with stimuli of much greater intensity—unless the anæsthesia be incomplete, and then excitation of seemingly any afferent trunk in the body may cause dilatation of the pupil. It must be remembered however in interpreting this result that stimulating currents applied to the efferent sympathetic division itself (or the cervical sympathetic trunk) in order to be efficient have to be stronger than those which are obviously efficient when applied to the nerves of the limb muscles. But it does not follow that to excite sympathetic afferent nerves stronger currents are requisite than for other afferent nerves, such as the cutaneous; it is certain some efferent sympathetic nerves (*e.g.* in the abdomen) are extremely easily excited. The converse of the above experiment, namely excitation of the central end of an afferent sympathetic branch of the spinal nerve is not easy to perform on the segment in question, because excitation of the central (lower) end of the cervical sympathetic has in my hands never yielded the slightest evidence of the existence in that trunk of any afferent fibres[2]. But Dr Bradford informs me that in vaso-motor

[1] A second paper will deal more fully with spinal vesical reflexes.

[2] Cf. Budge and Waller, *Compt. Rend.* 1851.

experiments he finds a much greater effect upon the blood-pressure follow excitation of the whole afferent root than follows excitation of its 'somatic' portion only, an observation which practically supplies the evidence which was wanting.

An objection to the 'synergetic' theory of the formation of the motor root is that the view presupposes, or infers, that mere spatial juxtaposition possesses curiously high value in the spinal mechanism of coordination. Are the separate spinal and the bulbar elements of the respiratory centre less perfectly associated in function because in the nervous axis they are placed apart? Similarity of quality rather than proximity in space ensures the harmony of their reactions.

Probably as clear evidence as any obtainable on the significance of the arrangement of the fibres of the motor roots of the limb-plexus would be obtainable from study of the peripheral distribution of the fibres composing the fellow afferent roots. If the arrangement and peripheral distribution of the fibres of the motor roots is based on functional coordination of action, not on morphological metamerism, then surely the same principle will pervade the peripheral distribution of the corresponding afferent roots as well. It is hardly possible to suppose that the distribution of the ventral root of the spinal nerve has been determined chiefly by physiological requirement, while the distribution of its dorsal (posterior) root has been determined by anatomical. I will not here attempt to enter upon any description of the peripheral distribution of the afferent roots of the limb as it is my purpose to devote a separate paper to that subject, but I will say that the results I have met with in experiments on the distribution of the posterior roots in Macacus agree in their broad features with those sketched in the posthumous papers left incomplete by Türck, who worked upon the Dog (1858). They disclose a metameric arrangement so absolutely anatomical, not functional, in significance as of itself to leave in my own mind no doubt as to morphological and metameric conditions being the true key to the muscular distribution of the efferent spinal roots as well.

If existent functional association is urged as the reason of community of root-supply for two muscular fibres or for two points of sentient surface there seems to underlie the argument a tacit assumption that a greater nervous resistance would be interposed between the two fibres or points were they to be innervated by adjacent roots instead of by one and the same. This supposition, as mentioned already, appears to me to possess no very secure basis in fact.

More intimate association would be expected between the one side and the other side of the hollow of the sole or palm than between for instance one edge of the sole and the top of the shin, or between one edge of the sole and the back of the thigh, or one edge of the palm and the skin on the inner side of the olecranon. The outer and inner sides of the sole and palm are points of surface which must be associated together with innumerable frequency and must with innumerable frequency enter consciousness together as parts of a consentaneous field of contact. The same can not so well be said of two such points of surface as the sole and the front of the shin or the sole and the back of the ham, or the side of the palm and the back of the elbow. Yet one lumbar root supplies the inner region of the sole and not its outer region, another supplies the outer region of the sole and not its inner region; one brachial root is distributed to the ulnar side of the palm and not to the radial, another to the radial side of the palm and not to the ulnar. And on the other hand one and the same lumbar root (5th) supplies at once the skin of the inner part of the sole and of the front of the shin, another (7th) the outer part of the sole and the side of the back of the thigh, and one and the same brachial root the ulnar part of the palm and the skin at the side of the olecranon. Would existent functional association order the distribution of the fibres of an afferent root in these ways? And this arrangement difficult to meet by the hypothesis of existent functional association is of obvious history and meaning if it be taken as part of the metameric segmentation of the limb, the limb being conceived a group of fused rays, portions of the metamerically arranged segments of the body.

Contrary to Panizza's doctrine, revived and ably re-appointed by Remak and by Ferrier and Yeo, and followed since by Bert, Marcacci, and others[1], I believe John Müller to have been right in attributing to the arrangement of the motor roots of the limb plexus an anatomical significance based on metamerism rather than a teleological dependent on supposed demands of functional coordination.

It will be seen that a hope with which the experiments in this paper were commenced is therefore disappointed. By analysis of the complex of fibres constituting the motor root one does not necessarily arrive at analysis of the muscular combination habitually employed for some particular coordinate movement of the limb.

[1] Dr R. Russell's paper from Mr Horsley's laboratory appeared since this was in type.

Section VI.

The general features of distribution of the motor nerve-roots to the musculature of the limb.

The above observations confirm therefore the facts first clearly stated by Eckhardt. Eckhardt wrote concerning the frog's plexus, "A great number of muscles in the limb obtain nerve-fibres each of them from several nerve-roots. Most of the thigh muscles almost always, some of the leg muscles frequently, are supplied by three, the latter more often by two nerve-roots." In Rhesus there seems but one muscle of the lower limb that receives its nerve-supply from a single root, viz. the tensor vaginae femoris, from the 5th lumbar; and sometimes one finds that muscle distinctly obtaining fibres from the 4th as well.

When a muscle is supplied by three nerve-roots it is noticeable that the middle root of the three usually causes the most powerful contraction. This is well exemplified by the tibialis anticus and the 5th, 6th, and 7th roots. Many other examples could be cited illustrating the point, and it may be accepted as a general rule. The upper and lower limits of the region of outflow of motor fibres to some muscles are more abrupt than to others, *e.g.* the lower end of the outflow to the precrural muscles is more abrupt than the lower end of the outflow to the intrinsic palmar muscles. If the "lift" in the isotonic myogram be taken as a rough measure of the amount of nerve supply from a given root, the relative quantity of innervation contributed to the tibialis anticus by each of the three above-mentioned motor roots in Macacus rhesus may be estimated.

With a load of 50 grms. and a lever multiplying 10 times, excitation of 5th root gave 42 mm., of 6th root 65, of 7th root 60. In another individual upper half (approximately) of 5th root gave 12, lower half of 5th root 40, upper half (approximately) of 6th root 48, lower half 41, upper half (approximately) of 7th root 45, lower half 19.

In the lower limb one finds for each muscle the outflow of efferent fibres to it spread unbrokenly over a certain considerable longitudinal region of the cord. I mention this because a different arrangement holds for the bladder and iris muscles, and because Peyer and Krause for the *pronator radii teres* of the rabbit found an outflow of fibres in the 7th cervical root, and in the 1st thoracic root but not in the intervening root of the 8th cervical nerve. This observation appeared curious enough to demand repetition, and I have repeated it twice and found on each occasion that the *pronator* in the rabbit is no exception to the general rule because it may be innervated from the 8th cervical as well as from the 7th, and the 1st thoracic.

In the great majority of instances muscles innervated by the same nerve-root lie adjacent one to another, so that a continuous sheet, or band, or ray of muscular tissue is supplied by the same nerve-root. Among the sacral nerve-roots an exception to this rule for distribution is certainly met with not infrequently in the case of the lowest filaments of the 8th subthoracic root, or the entire 9th subthoracic root. These are then distributed to the sacro-coccygeal muscles on the one hand and on the other to intrinsic muscles of the sole, far distant from the sacro-coccygeal muscles. It must not be thought that this is merely a separation between the regions of distribution of the *dorsal* division of the nerve-trunk on the one hand and of the *ventral* division of the nerve-trunk on the other. When the dorsal division of the 9th nerve has been cut through, on exciting the anterior root a considerable portion of the sacro-coccygeal muscles still act, and the sphincter ani still acts, together with short muscles in the foot. Among the sensory roots a similar divided area of distribution was found for the 2nd and 3rd thoracic nerves of the dog by Türck. In the monkey I have not been able myself to confirm the existence of divided skin fields for the distribution of either of those nerves, on the contrary I find that each of them in Macacus possesses a continuous field of distribution.

Forgue and Lannegrace draw attention to the fact that the muscles of the outer aspect of the leg, the *peronei* are supplied by *one* root only, the 7th, and they relate the frequency of peroneal atrophy to this fact. Ferrier and Yeo say of the peronei that they are not thrown into contraction by the 7th root, but that they are by the 6th. In my own experiments the evidence has been clear that the peronei are supplied by both the 6th and 7th roots. They can be excited from the cortex through those roots. Excitation of the 6th root gives contraction especially of the peroneus longus, of the 7th root especially of the peroneus brevis. The 5th root also has on twelve occasions, when the plexus has been of the high type, supplied the peroneus longus. That the 5th root supplies the peroneus longus is shewn also by the fact that where two months previously the 6th, 7th, 9th and 10th roots have been divided, peroneus brevis was found atrophied and no contraction of it could be obtained on excitation of the nerve belonging to it, while the longus replied fairly well to excitation of its nerve, although it was somewhat atrophied as compared with the sound side. That the brevis receives fibres from the 7th root is clear from the fact that it replied well to excitation of its nerve when the 6th, 8th and 9th roots had been divided two months previously, although it was somewhat atrophied as compared with the muscle of the sound side. It must be mentioned however in the former experiment (section of 6th, 7th, 9th and 10th roots) that although from neither the nerve to the peroneus brevis nor from that muscle itself any reply except widely removed from the normal could be elicited by electrical stimulation, yet in the nerve itself a considerable number of intact nerve fibres existed, although the degeneration had run a two months' course. (Intact large fibres in the nerve trunk close outside the muscle, 98, intact small fibres, 71; but the nerve fibres remaining in the nerve trunk were some quite large, some quite small and some of various sizes intermediate).

Ferrier and Yeo found that the *flexor longus hallucis* was supplied from 6th and 7th subthoracic roots, the *flexor longus digitorum* from the 7th root only. In my own experiments I have found in the *postfixed* type of plexus both muscles supplied from the 6th and 7th, occasionally slightly from 8th also; in the high type of plexus from the 6th and 7th, and slightly from the 5th also.

Forgue and Lannegrace make the 6th root supply both the *psoas* and the *biceps*. In my own experiments I have never observed the psoas and the biceps to be excitable through one and the same nerve-root. In other words I possess no evidence of an overlap of the outflows of fibres to these two muscles. The lowest point to which the outflow of the fibres for the psoas has ever descended in my experiments is about half way down the region of the 5th root. The highest point to which the outflow for the biceps has ever ascended is about half way up the region of the 6th.

It is curious to notice that the external head of the *gastrocnemius* seems to be innervated from a set of root-filaments lying more anterior than do those for the internal head. The outflow to the external head is represented less in the rootlets of the 8th than is the outflow to the internal head; in the rootlets of the 6th it is more abundant than is the outflow to the internal head. After division of the 6th and 7th roots it atrophies much more than does the internal head. After section of the 6th and 8th roots it does not suffer atrophy obviously more than the internal head, excitation of the muscular nerves to each giving a fairly good contraction.

The innervation of the inner head of the gastrocnemius appears to be extremely similar to that of the *soleus*. The external head has an out-flow which extends further forward (upward) than that of either the internal head or of the soleus. The *plantaris* receives less fibres from the 5th than does the outer head of gastrocnemius, and approximates toward inner-head and soleus. The peronei judged from their root supply belong to the anterior rather than to the posterior musculature of the leg, although they are extensors of the ankle-joint.

The *accessorius* of the foot appear to have a less share in the 9th root than does the *adductor hallucis*, when the 9th root supplies both these muscles. Of all the muscles in the limb the *tensor vaginae femoris* has seemed the only supplied by one nerve-root alone; in three experiments it was thrown into slight action by the 4th as well as into strong action by the 5th.

The remarkable fact that the external or short saphenous nerve, a nerve described as purely sensory by all authorities without exception as far as I have found, does in Macacus rhesus contain motor fibres for the plantar muscles of all the pedal digits has been already mentioned. I have not yet fully analysed the root constitution of the branch. As regards afferent fibres it contains constituents from the 7th root more abundantly than from the 6th, from the 6th more abundantly than from the 8th (1st sacral). It appears to contain motor fibres from the 7th and 8th and often 9th roots, so that whether the nerve-trunk to the plantar muscles descends in front of the mass of the great sural triceps or behind it the final connections of muscle-fibre and nerve-root remain the same whichever route is taken. Despite the extraordinary amount of individual variation already discussed above the connection between the position of the central starting-point (the nerve-root) and the peripheral end-station (the muscle-fibre) is therefore for the same parts in the same individual definite and fixed enough.

As regards the posterior limit of the region of outflow of motor-fibres to the skeletal muscles of the lower limb it will be seen that according to my own experiments the limit is reached at the same place in the rabbit, the cat, the dog, the Rhesus and the Bonnet monkey, namely, usually in the 9th, less frequently at the lowest edge of the 8th sub-thoracic root—a variation, the extreme limits of which lie about three millimeters apart on the surface of the cord. As to the relative frequency of occurrence of the *postfixed* and *prefixed* types, that can in result of this variation be distinguished, in the rabbit and dog my experiments are not numerous enough to afford basis for a conclusion; in the cat the extension into the 9th seems about equally common with its absence. In Macacus the two forms seem to be about equally frequent. In Rhesus I have noted 37 examples of the *postfixed* plexus, 29 examples of the *prefixed*, in Bonnet 3 examples of the *postfixed*, and 5 examples of the *prefixed*. It is of interest that in several instances the type of brachial and crural plexus was coincidently examined and ascertained in one and the same individual and four times a prefixed type of sacral plexus was found accompanying a postfixed type of brachial plexus. By far the most usual place for the posterior limit of the outflow of motor fibres to the fore-limb has been in my own experiments on the rabbit, rat, and macacque at the 2nd thoracic root, but not so in the cat and dog, in which animals the limit usually lies at the 1st thoracic.

As to the downward limit of the motor outflow for the lower limb my experiments indicate that both Forgue and Lannegrace, and also Ferrier and Yeo, are right in the positions they assign to it; that is to say the limit may fall at the place given by each pair of observers, but it may be that in Macacus the limit found by Ferrier and Yeo is somewhat more usual than that found by Forgue and Lannegrace.

As to the downward limit of the motor outflow for the upper limb the experiments completely confirm the limit set by Ferrier and Yeo in their later note when they placed it at the 2nd thoracic root; Forgue and Lannegrace err in placing it at the first thoracic. For the motor outflow to stop short so high must be, to judge by my own experience, a most rare occurrence. I have only met with one dubious instance in thirteen experiments.

I find, contrary to Peyer and Krause, that the 2nd thoracic in the rabbit gives motor fibres to the limb, especially to the muscles of the hand. In the rat also the 2nd thoracic root contributes to the brachial plexus, and gives, on excitation, flexion of the digits. In the cat and dog although not usually so, in the former animal I have once met with it.

In the horse[1], in the rabbit[2], and in Macacus[3], the 2nd thoracic gives a branch of insignificant size to the brachial plexus. Krause, who did not notice the existence of the branch until he had published experiments on the functions of the roots of the plexus, dismisses its physiological value as safely negligible. Had he examined it physiologically he would certainly have found that it ran down to the very apex of the

[1] Chauveau, 1854. [2] Krause, 1868. [3] Brooks, 1883.

limb and supplied with motor-fibres the intrinsic muscles of the hand, with sensory fibres the inner aspect of the upper arm. Ferrier and Yeo shewed that in the monkey it supplies motor fibres to the interossei of the hand. In Macacus rhesus besides the above distribution I have in three individuals found it supplying the pronator quadratus and the flexor perforatus, and the ulnar part at least of the flexor perforans, in the fore-arm as well as the intrinsic muscles of the hand. As to skin, it usually, as I shall shew in dealing with the sensory roots of the limb in monkey, supplies the skin from below the axilla to far below the elbow. In the Bonnet in two individuals I have also found it supplying the flexor profundus, flexor sublimis and pronator quadratus as well as the muscles of the hand.

J. D. Cunningham in 1877[1] recorded the result of an examination of the constitution of the human brachial plexus in thirty-seven subjects. In twenty-seven of these he found the branch now under consideration passing into the plexus from the 2nd thoracic root, as well as the invariable branch from the 1st thoracic to the plexus. There can I think be little doubt that in man in a large number of individuals the 2nd thoracic nerve supplies motor fibres to the intrinsic flexors of the hand, and, perhaps less often, to the flexores digitorum and the pronator quadratus as well. That in man both the 1st and 2nd thoracic roots contribute largely to the motor innervation of the intrinsic muscles of the hand I cannot hesitate to believe, in spite of the fact that Herringham failed to trace fibres from those roots so far outward as the hand. It must be remembered that Herringham had the difficulty of treating the 8th cervical and 1st thoracic roots as a conjoined cord. It will be seen from the above that the branch from the second thoracic root to the brachial plexus is as regards its motor functions strikingly analogous to the branch from the second sacral to the great sciatic in dog, cat and Macaque. I have however never found the 9th sub-thoracic of Macacus (the 3rd sacral of man) supply a deep muscle of the leg, certainly not the flexor longus digitorum.

As regards the lower limb Ferrier and Yeo conclude that in man the 2nd sacral root is the lowest which contributes motor fibres to the limb. They conclude so because in the monkey the 1st sacral root (of that animal) appeared to be the lowest root to do so, and the 1st sacral of the monkey is the same nerve as the 2nd sacral nerve of man. But Forgue and Lannegrace found the 2nd sacral of the monkey supply

[1] *Journ. of Anat. and Physiol.* XI. iii. p. 539.

the foot muscles, and my own experiments shew that although not always so it is so very frequently.

It is curious however, that in spite of this difference in the experimental results of the two pairs of investigators, Forgue and Lannegrace adopt the same nerve-root as do Ferrier and Yeo for the most posterior, which in man contributes to the muscles of the lower limb; they, like Ferrier and Yeo, arrive at the 2nd sacral root of man, but reach it by a different path of argument. Believing that in the monkey it is the 2nd sacral root they take the 2nd sacral of the monkey to be the same root as the 2nd sacral of man, an opinion in which they stand alone, and have in my opinion a large balance of good evidence against them. In view of my own experiments the probability amounts in my own thinking almost to certainty that in man the lower limit of the motor outflow to the intrinsic muscles of the foot and that is to say to the whole lower limb does often, though not always, extend into the 3rd sacral root.

It seemed desirable to learn with more exactitude to which one of all the several muscles of the limb those motor nerve-fibres belong that in their exit from the spinal cord are the most posterior of the whole series destined for the skeletal musculature of the limb.

Although as already several times insisted upon in this paper the general scheme of distribution of the spinal roots to the limb musculature reveals lines or rays composing the limb and passing from the attached base of it outwards along its length, previous experiments have shewn the somewhat surprising fact that the intrinsic muscles of the hand and foot are innervated from nerve-roots lower (more posterior) than those supplying any of the muscles of the forearm or the leg, and of the upper arm or thigh. This arrangement appeared so contrary to the arrangement which one finds holding good in the distribution of the afferent nerves to the skin of the limbs that I desired to examine with special care the facts affirming it.

The question to attempt seemed this; the limb consisting of an attached base and three serial parts, a proximal, a middle and a distal, is there no muscle or piece of a muscle either in the proximal or in the middle part of the series which receives a motor supply from root filaments at least as posterior in their place of outflow from the spinal axis as those that supply the intrinsic muscles of the distal portion of the series? Or, stated according to the explanation of the construction of the limb to which I adhere, in the limb musculature is there no vestige of the proximal piece of the long hindmost ray, the distal part of which is well preserved in the muscles at the free end of the member? Of the most proximal piece of the ray, that namely in the attached base of the limb there survives a muscular portion as part of the glutei. As to the rest? In Rhesus one finds that excitation of the lowest (most posterior) nerve-root entering the limb plexus evokes contraction of the intrinsic muscles of the distal segment, and in the case of the upper limb[1] the pronator quadratus and also both long flexors of the fingers. In the case of the lower limb occasionally the soleus in a questionable (but in cat sometimes unquestionable) manner contracts. Is there no small part of these muscles which is demonstrably at least as posterior as the intrinsic muscles of the hand and foot? In Rhesus one had not long to wait for an opportunity of seeing that when what I have termed the *postfixed* type of plexus is slightly departed from by an upward shift the only motor nerve-fibres in the outflow from the most posterior of the spinal segment supplying the limb muscles pass to the intrinsic muscles of the foot and hand, especially to the interossei and the short flexors. These muscles contracted, while neither by inspection, touch, nor the myograph could any contraction of any part of the exposed soleus or of the pronator or flexores longi digitorum be made out.

In the same way in the cat individuals may be found in which excitation of the 9th sub-thoracic anterior root evokes no contraction of muscles in the limb, except in the distal segment where flexion of the proximal phalanges with extension of the distal phalanges is seen and persists on excitation of the root after division of all the structures at the ankle-joint excepting the posterior tibial nerve and blood vessels. The outflow of motor fibres to the intrinsic muscles of the distal segment of the limb does therefore as shewn by these cases extend further posterior than the outflow to any other muscle situated wholly within the limb.

To which of the intrinsic muscles themselves does the motor root-filament pass which arises (as regards a superficial origin) lowest (most posterior) in the cord of all those going to the limb?

A glance at the form of the well-developed mammalian limb suffices to awaken the idea that the pollex and the hallux belong to the anterior or preaxial edge of the appendage, and the fifth digit to the posterior or postaxial edge. This idea is suggested by numerous facts of which it is unnecessary to attempt a recapitulation here. The dissections of Herringham afforded striking exemplification of the degree to which

[1] Sherrington. *Proc. Physiol. Soc.*, Feb. 13, 1892.

careful examination of the parts can be made to reveal evidence of the mutual anterior and posterior, pre-axial and post-axial, relationships of the small individual parts comprised in even the distal segment itself. Experiments confirmatory of Herringham's observations had shewn me that both in Rhesus and in Cat the cutaneous nerves display in a striking manner the preaxial and postaxial relationships of one digit to another[1]. But from the nerve supply of the muscular elements of the limb, I have sought almost in vain for evidence of a similar arrangement. I expected that in the hand and foot of the monkey such evidence might be well obtained because of the fine divisions of the musculature in them and because of the series of intrinsic muscles being in them arranged parallel with the axis of the limb and therefore ranging from the preaxial to the postaxial borders. In Macacus rhesus the movements of the foot, hallux, and digits are particularly free, more so than in the Bonnet and in many monkeys; there could not seem a better subject for analysis of the problem. Excitation of the 6th, the 7th, the 8th or the 9th sub-thoracic roots each causes contraction of the intrinsic muscles of the foot. The upper three of these nerve-roots are very large and their component fibre-bundles, the rootlets of the root, spread like the ribs of a half-closed fan from their point of common investment by the dura to the line of their attachment to the spinal cord. The rootlets can easily be used for isolated excitation as in experiments described above. Will excitation of the most anterior filaments have a different effect upon the muscles of the foot than excitation of the most posterior?

Experiment. 13. iii. 1890. Rhesus Macacus. Strong female. A.C.E. mixture. Right side. At the ankle the following tendons divided; *Tib. anticus*, *Ext. dig. et hall.*, *Peronei*, *tendo Achillis*, *Flex. long. dig. et hall.*, *Tib. posticus*. The plantar nerves cut, the musculo-cutan. and anter. tibial nerves remaining. Left side tendons divided as on right. The anterior tibial nerve and the musculo-cutaneous nerves cut. The blood vessels not interfered with, nor the external and internal plantar nerves. The spinal cord is exposed at the level of the crests of ilia and above and below that level for a short distance. The dura mater is then slit at the roots of the ninth and eighth subthoracic nerves right and left, and the posterior roots of those nerves cut through near the ganglion, followed upward, and excised. The anterior roots of the nerves are exposed, consisting as usual of a considerable number of fine rootlets; these can be even further subdivided by dissection but at the risk of damage to the nerve fibres. In the right 7th nerve ten natural bundles are

[1] Cf. also Langley on Sweat Nerves, this *Journal*, Vol. XII. p. 347.

taken, in the right 9th, 3 natural bundles; each of these is ligated close to its exit from the spinal cord, and has a length of about five centimeters; can be lifted well up in the wound.

Time, 3.50. Stimulation with minimal efficient currents, the secondary coil is at 29 cm. from the primary, the currents are just perceptible to the tongue when the secondary is at 16·6 cm.

3.54. Highest filament of 7th root; abduction and extension of hallux; extension of all the digits; the movement of the minimal digit seems as sharp and evident as that of the hallux.

3.57. 2nd filament: same effect.
3.58. 3rd " "
3.59. 4th " "
4.1. 5th " "
4.3. 6th " "
4.4. 7th " "
4.8. 8th filament: same effect.
4.9. 9th " "
4.12. 10th same effect: no difference between action of minimus and hallux.

4.15—4.21. The effect of the highest and lowest filaments of the 8th compared in their effect upon the hallux, and no difference discovered. The minimal current for movement of the hallux is with the secondary at 29 for the highest filament, with the secondary at 29·5 for the lowest filament.

4.22—4.26. Compared as to effect on the minimal digit, the same numbers obtained as for the hallux. 4.28. No movement of the toes or hallux obtained from any of the three filaments of the 9th nerve.

Left side; of the filaments of the anterior roots of the 7th and 8th sub-thoracic nerves, nine natural bundles taken, ligated and isolated in the same way as on the right side; the rootlets of the 9th taken as four filaments. Secondary coil at 29 cm.

4.44. Highest filament of 7th gives adduction and flexion of hallux, with flexion of all the digits of minimus as much as of rest, and hollowing of the sole.

4.47. 2nd filament: same effect.
4.48. 3rd " "
4.48. 4th " "
4.50. 5th " "
4.51. 6th " "
4.53. 7th " "
4.54. 8th filament: same effect.
4.56. 9th " "
4.58. 1st fil. of 9th " "
5.0. 2nd " " "
5.1. 3rd " " "

5.2. The highest filament of the 8th is then compared for its effect on the hallux with the lowest of the 9th and no difference detected. Same result on comparing their action on the minimal digit.

I had not anticipated that the experiment would yield the above result. It is however similar to three others made with the same object in view; the same result was yielded by all made. Two of the experiments included the anterior roots of the 7th and the 8th in a series of 18 filaments examined. No experiments have been made in the cat and rabbit because of the lesser mutual independence of the digits in those forms. The above observations are however strengthened by similar on other nerve-roots, although not on roots so suitable for minute analysis of the functions of the root-filaments as are the 2nd and 3rd sacral. The highest and lowest rootlets of the 6th lumbar have given several times when isolated and excited, an apparently identical effect. It would therefore appear that with certain limitations[1] the stimulation of a rootlet of an anterior root gives the same qualitative results as does stimulation of the entire root; all the muscles which excitation of the entire root causes to contract, are made to contract also by excitation of any one of the rootlets into which the entire root is naturally subdivided. In other words the commingling of the motor fibres to various muscles is great even at their very exit from the cord, and each of the natural rootlets of the root consists of an aggregate of fibres often representing as far as the skeletal muscles are concerned all the groups of nerve-fibres contained in the entire root. "The individual bundles of the anterior root are in miniature the entire root itself and give results in quality broadly the same as does it, although not in quantity[2]." This commingling of different nerve-fibres at their very exit from the cord points to a probability of their sources of origin within the cord being also commingled in the transverse plane of the cord if not in the longitudinal.

Although the commingling which thus occurs affects each constituent rootlet of the spinal root, and appears to make each filament to a great extent a miniature of the entire root itself, in certain segments of the cord the existence of marked individual differences in the functions and distribution of the root filaments are easily discoverable.

In six of the experiments dealing with analysis of the filaments composing the anterior root of the sixth nerve the following results occurred. The series of filaments composing the root had been in each case parted into the small natural bundles. These may be numbered from above downwards, 1, 2, 3, 4, 5, 6. In one case 6, 5, 4, and 3 were found to give contraction of the intrinsic muscles of the foot, the flexors predominating in the action upon the digits, whereas bundles 1 and 2 supplied no intrinsic muscle of the foot. In the other 6 and 5 gave contraction of the intrinsics of the foot while 4, 3, 2 and 1 did not.

[1] Sherrington, *Proc. Physiol. Soc.* Feb. 1892, p. viii.
[2] Sherrington, *Proc. Physiol. Soc. loc. cit.*

Each result was repeated many times on the occasion and precautions taken to avoid escape of current, the whole intradural length of the 5th, 7th and 8th roots in each case being completely excised. Under all the precaution taken the same result recurred unfailingly on these two occasions. Very frequently the sixth anterior root contains no fibres to the intrinsic flexors of the foot, and the three exceptions above occurred in individuals in which the plexus was certainly not so low as in the typical conformation of the *postfixed* pattern.

Again on two occasions in which the intrinsic flexors of the digits were not represented in the 9th anterior root, the 8th anterior root on being split into five filaments gave evidence that the short flexors were represented without the soleus and the gastrocnemius in the lowest filaments, but in the upper filaments the soleus and gastrocnemius as well were present.

Again excitation of the two lowest (most posterior) of eight filaments into which a 6th anterior root had been separated gave extension of the ankle; while excitation of each of the remaining six gave flexion of the ankle.

Again the higher (more anterior) filaments of the 7th will sometimes give a better action of the short extensor of the 2nd toe than do the most posterior filaments of the 7th. And the most posterior filaments of the 5th give a better extension of the hallux than the more anterior filaments of the 5th.

Again on two occasions the motor outflow to the internal group of thigh muscles, supplied by the obturator nerve, has had its lower limit about one-third of the distance up the 5th lumbar rootlets, the root filaments below that point passing to the semimembranosus and the pretibial muscles, but not to the adductor group.

In one experiment the extensor muscles of the thigh were represented in the upper half of the rootlets of the 5th lumbar segment, but not in the rootlets of the lower half.

The deep inner hamstring is frequently represented in the lower but not the upper half of the 5th lumbar segment.

It is curious to note that the region of outflow of the efferent fibres to a group of muscles or the representation of a particular movement at a joint often ends not conterminously with the spinal segment but somewhere within the spinal segment either as it were overstepping or falling short of the anatomical limits of a segment. The representation then stops short not at the interval between two segments of the cord, but midway within a segment of the cord. This fact may modify considerably our conception of the spinal root as a guide in studying the segmental arrangement of the limb, and on the other hand our conception of the morphological construction of the limb itself. The ankle and wrist, which seem at first sight natural boundaries marking the division between fundamentally distinct portions of the limb, are not regarded as such in the segments of the spinal cord. On the sensory side much evidence of a similar kind is obtainable, and I will reserve the point for discussion in a paper dealing with the sensory evidence.

E. Remak[1] concluded that most muscles are represented in the cord by vertical tracts, so that as Gowers[2] remarks the whole anterior grey matter at any one nerve segment contains cells that are concerned with different movements. The length of the region of outflow of motor fibres for certain primary movements in the lower limb of the species *Rhesus* may be thus tabulated, the table being formed by combining the results from various individuals.

	11	10	9	8	7	6	5	4	3	2	1
Hallux											
Flexion			—	—	—	—					
Extension					—	—	—				
Digits											
Flexion			—	—	—	—					
Extension					—	—	—				
Ankle											
Extension				—	—	—					
Flexion					—	—	—				
Knee											
Flexion				—	—	—	—				
Extension						—	—	—	—		
Hip											
Extension			—	—	—	—					
Flexion							—	—	—	—	
Adduction						—	—	—	—		

It is clear that the region of outflow for movement at the hip is longer than that for movement of any other joint in the lower limb, especially than for that of the ankle. It runs through at least seven segments of the cord instead of four. But if each of the main movements of the joints be considered individually it is seen that the region of representation in the spinal roots of

[1] *Arch. f. Psychiatrie*, Vol. IX.
[2] *Dis. of the Nervous System*, Vol. I. p. 192. 2nd edit.

Macacus is as long in the case of the small joints of the toes, such as the metatarso-phalangeal of the thumb, as it is for the hip or knee, or ankle. It is noticeable that with all the joints mentioned the region of outflow for any individual main movement extends into at least three segments of the cord. The long region of outflow for movement at the hip is due to the *flexion* outflow being more separated from the *extension* outflow in the case of the hip than in the case of the other joints, especially than in the case of the joints of the digits. One might express the difference by saying that the spinal nuclei for flexion of the hip and for extension of the hip overlap each other very slightly, but that the nuclei for flexion and extension of the digits overlap each other very largely.

This fact is merely the physiological side of an anatomical disposition of the musculature limb which has considerable morphological significance. In the proximal portion of the limb (the thigh) the nerve-roots supplying the musculature are not common to muscle-groups both of the anterior and posterior aspects of the limb. But the nerve-roots entering the foot and leg each supply muscles both on the posterior and anterior aspects, more markedly so in the foot than in the leg. In the foot the dorsum is distinctly segmentally anterior to the sole; and there the rule is broken (and the same may be said of the hand) by the lowest root which enters the foot or hand frequently supplying the musculature on one aspect only, that aspect always being posterior, the plantar or palmar—unless by some straining of anatomical principle the dorsal interossei may be considered to belong not to the plantar but to the dorsal side.

The representation in the spinal roots of the opposite movements at the limb-joints is an overlapping one, and as above mentioned the overlap is greatest for the distal joints of the limb. In the case of the phalangeal joints the overlap is so considerable that the action of the more powerful set of muscles (the flexors) in some individuals completely overcomes the less powerful extensors in the movement given by each one of the several entire roots distributed to the muscles of the joint. In these cases there is no spinal root which on excitation gives extension of the digits, but there are four which each of them yield flexion.

Of the opposed movements of joints the one directed toward the anterior aspect of the limb has always a spinal representation more anterior in the spinal nerve-roots than is the representation of its fellow movement of opposite direction.

In estimating the position of any limb-muscle from the point of view of its supply of efferent fibres from spinal roots, it is the situation in the limb of the fleshy part of the muscle that will be found a guide to the nerve-roots likely to innervate it. The tendons of anatomical "attachment" of the muscle appear in this relation to be of little importance. What may be the exact part moved by the muscle, or what may be the joint at which movement is produced by the muscle, appear not to materially enter into the question. When for instance experimental excitation is applied to the ventral roots of the lumbo-sacral nerves in successive order from below upward, the successive excitations are found to evoke from the hallux in their ascent along the cord at first, that is, from the lower segments, the characteristic flexion at proximal joint (with adduction) this movement on exciting higher segments gives way to a movement still nearer the extremity of the limb, namely, to flexion of the extreme tip of the digit. The long flexor of the hallux is inserted into the terminal phalanx of the hallux, the short flexor into the proximal; flexion at the terminal joint is the movement characteristic of the action of the long flexor, flexion at the proximal joint is the movement characteristic of the short flexor. Inasmuch as the musculature becomes myomerically more posterior as we pass down the limb from the attached base to the free apex of it we might have supposed that motor fibres for flexion at the terminal joint of the digit would in the spinal cord lie posterior to those for flexion of the proximal joint. But the reverse is the case. The muscular fibres which flex the terminal joint are innervated from a point of the cord anterior to that which innervates the muscular fibres for flexion of the proximal joint, because the former mass of muscle fibres is situated nearer the attached base of the limb than is the latter mass. Of the two movements that which would from its character (direction, joint affected, &c.) claim to be the more posterior is found in reality to be the less posterior, in accord with the situation in the limb-musculature of the fleshy belly concerned. This circumstance seems to argue with some force the probable correctness of the view advocated in the present paper, viz. that the arrangement of the limb plexus rests on a basis of anatomical rather than of functional nature, the key to it therefore is to be sought rather by consideration of anatomical facts than by conjecture as to the functional moment of individual muscles. We must consider the limb to be an organ of segmental structure, and that, plastic like the rest of the body, it has been moulded by variation and by function, but not so rudely as to seriously obscure its segmental plan.

In judging of the question whether a muscle when supplied by several nerve-roots is supplied by them in such a way that one piece of the muscle is supplied by one root, another by another, there is certainly great interlapping of regions belonging to the individual roots, but I would not go so far as to say with Forgue and Lannegrace, "Excitation of a spinal root determines in the muscles which it supplies a total, not a partial contraction. The tributary fibres of the root are disseminated through the muscle supplied by it and not 'cantonnée' in a special zone of it." In the small muscles of the foot and hand their appearance during contraction certainly completely countenances that view; the view can however I take it only be securely asserted after a lengthy series of degeneration experiments has been carried out. On the other hand simple inspection is enough to convince one that in the case of some of the larger muscles, *e.g.* in thigh and spinal regions, the nerve supply from the different roots is distinctly "cantonnée;" a district of the muscle will belong to this root, another district to that root, it always being remembered that the limits of the districts have a large mutual overlap. Thus a thigh muscle often seems to have when thrown into contraction by excitation of the spinal roots supplying it two or three separate foci of contraction, one for each spinal root, centres at which the contraction is first detected as excitation of the root is produced by gradually passing from subminimal to minimal stimuli, centres at which the contraction is most powerful when fully efficient stimuli are used. Striking examples of this phenomenon are yielded by the sartorius muscle and the 3rd and 4th lumbar roots. Minimal excitation of a filament of the 3rd root will give contraction limited to the upper part of the sartorius. Minimal excitation of a filament low down in the 4th root will give contraction limited to the lower part of the sartorius. So also in the biceps, minimal excitation of the 8th root gives contraction limited to the more superficial part of the muscle; minimal excitation of the 6th root gives contraction limited to the deeper part of the muscle. In the superior sacrococcygeus of the cat minimal excitation of the 7th root gives contraction of a zone of the muscle distinctly different from and nearer the head than the zone of contraction producible through the 8th root; and the zone belonging to the 8th root lies further headward than the zone belonging to the 9th. In the same way the psoas is innervated in a series of overlapping zones arranged in a fore-and-aft series along the longitudinal axis of the body, in the same way also the oblique and transverse muscles of the abdominal wall. The way in which at least certain muscles are innervated more or less in root-districts is shewn by the atrophies following root degeneration produced by section of the spinal roots. In an experiment in which the 6th, 7th, 9th, and 10th sub-thoracic roots of Macacus were divided on the right side, the pyriformis muscle on that side was found three months later to be so atrophied that the sciatic and pudic trunks, &c. lay bare to view from the pelvic aspect, a slip only, namely, the most mesial portion, arising from the first piece of the sacrum remained comparatively sound—the portion from the 7th lumbar completely wasted.

On the other hand in the muscles of the sole it is difficult to detect more than dubious hints of such an arrangement. Minimal excitation of the filaments of the 9th root produces localised contractions of certain plantar muscles, especially of hallux, index, and minimus, which are often indistinguishable from similar contractions following minimal excitation of the filaments of the 8th and the 7th roots. In my experiments flexion of the hallux has been the most usual result of minimal excitation of any of these three roots, next in frequency has been slight flexion of the minimus, next of the index, but on one occasion slight flexion of the 3rd and 4th digits together was much more easily obtained than even flexion of the hallux. The flexion of the hallux is usually accompanied by slight adduction and opposition. Of the existence of separate root-districts in any one of the intrinsic plantar muscles therefore I have not been able to get good evidence. On six occasions I have left only the lumbricales and interossei and the adductor hallucis in connection with the spinal roots, eliminating in that way the action of the short flexors, &c. and each root that supplied one supplied all of these thirteen small muscles, and all in just about equal degree, *e.g.* the 1st lumbrical about as much as the 4th. Indeed when the musculature of the plantar region is taken as a whole the best evidence of separate root-districts at all existing in it is to be obtained from the abductor hallucis and short flexor digitorum, which in some individuals are thrown into contraction by the most posterior filaments of the 6th lumbar, without the lumbricales or interossei contracting.

I would conclude therefore that there is much greater over-lapping and intermingling of the root-districts in the muscles of the foot than in those of the thigh, and that in the former case the intermingling is so great as to warrant Forgue and Lannegrace's conclusion above quoted, but that their conclusion is not applicable to the larger and proximal muscles of the limb. To this point I shall return in a succeeding paper.

As to the question whether or no when a muscle receives nerve-fibres from more than one spinal motor root two of the nerve-roots, each of them, may supply fibres to one and the same muscle fibre, observations by Kühne, Krause, Eckhardt and others failed to give evidence of the multiple supply. It is true that observations on the point have generally proceeded along the lines of microscopical search, and the finding of many fibres that are not doubly supplied does not exclude the possibility of the existence of some that are. Yet my own experiments on the roots to the gastrocnemius and tibialis posticus, referred to above, seem to shew that if any fibres with multi-radical supply exist in those muscles they must be very few indeed. The seat of peripheral fatigue lies somewhere in the neuro-muscular content of the tubule of sarcolemmal membrane which encloses and isolates each individual muscle-fibre. If then in any muscular tubule a condition of fatigue has been produced by repeated excitation of it through a particular nerve-root, and if embouching into the same tubule there exists another conductor from a second nerve-root it would be expected that on closely subsequent excitation of this second root the contraction elicited would bear the characters of fatigue. But as shewn in the experiments (Fig. 9, Pl. XXIII.) the myogram given by them may when the circulation is still to some extent intact, be deformed to a slight degree only by the fatigue set up through the other root, and this slight deformation may well be referable to mere soakage of fatigue substances from the tired part of the muscle into the adjacent untired part.

Variation.

Excitation of the same spinal nerve-root does not always produce the same movement even in individuals of the same species, sex and approximate age. For instance in Rhesus, excitation of the 6th root produces in most individuals flexion at the knee, but produces in a few individuals extension at the knee. When one motor spinal root of the limb plexus has been isolated by section of the adjacent ones the paralysis is, as already mentioned earlier, not always the same for the same root in different individuals tested under experimentally similar conditions. Frequently in analysing the distribution of the component filaments of a root by excitation it is found that in different individuals filaments which correspond one with another in absolute position do not correspond in function.

These are but examples confirming and illustrating the statement of

Eckhardt[1] for the frog, that in the root-supply of the limb muscles "there is a good deal of individual variation," and that "when a nerve-root is unusually thick, the additional fibres in it are not all, perhaps none, employed in supplying the usual muscles with more fibres, but supply more muscles than the usual ones." The 9th sub-thoracic anterior nerve-root sometimes contains fibres to the muscles of the foot; and sometimes it does not. No trace of contraction of the muscles of the foot or leg could be elicited by excitation of the nerve-root, even when quite strong currents were used, and although movement of the tail and anus with depression of the perineum was produced by currents of very weak strength. It was noticed in those cases in which excitation of the 9th root did not give contraction of any muscles of the leg or foot, that excitations of the 5th, which usually give feeble extension of the hallux, sometimes gave good flexion of the toes, especially of the hallux. In these cases it was seen that the closure of the anus produced by excitation of the 9th root, which is usually very vigorous, was not so vigorous as usual; and that on the other hand there was more movement in the perineum than is usually the case on excitation of the 7th. In the frog, cat, monkey, &c. an inconstancy exists as to the segmental level of exit from the cord of the motor fibres for the limb muscles and others, and the inconstancy affects not one root of the plexus at a time but a number of them, so that if the outflow of the fibres, for instance for the long flexor of the hallux, extends into a nerve-root lower than it usually does, the upper limit of the outflow to that muscle will not extend into a nerve-root so high as that which it reaches usually.

This may mean that the motor nucleus of the long flexor of the toes is itself lying farther down, farther posterior in the cord, than its usual position, or it may merely mean that the efferent fibres from that nucleus descend in a longer intraspinal course than usual before they escape and become extraspinal in the root bundles.

To this point I have already alluded, but one induction from the facts is clear, namely, that the region of outflow of the fibres to the particular muscle although altered in relative position with regard to the nerve-roots is not altered in its relative length but remains of its own relative length. And this probably is true also of the motor nucleus itself.

From the above it is also clear for the motor mechanism of this part of the cord that generally if the region of outflow to one muscle lie

[1] *Loc. cit.*

higher than usual, the regions of outflow to other muscles lie also higher than usual, and vice versa. In example of this when excitation of the 6th root gives extension of the knee, the 9th root contains motor fibres to the foot muscles. When the outflow for the intrinsic muscles of the foot is placed higher than usual, the outflow for the extensors of the knee lies also higher than usual, and the outflow for the flexors of the knee also higher than usual.

This applies not only to muscles which are near to one another in place and kind but to muscles widely apart and widely different, *e.g.* when the outflow for the intrinsic muscles of the foot is high so is it also for the sphincter of the anus.

The shifting up or down of the region of outflow along a certain length of the cord appears to apply usually to all the efferent motor fibres of that length, that is to say, they all share in the displacement and about equally; in other words, although each is displaced absolutely, it is not displaced relatively to its neighbours.

It seemed desirable to see whether this rule held good for efferent outflows of so different a nature as those to the muscular coat of the bladder and the fine muscles of the digits.

Contractions of the bladder were therefore registered in two experiments in which the ninth nerve was found to contain no flexors for the toes or foot, and the results obtained in each when compared with others previously obtained (vide supra p. 678) shewed that where the region of outflow for the foot muscles was higher than usual the region of outflow of the efferent nerves for the bladder was also higher, *i.e.* strong in 8th root, weak in 10th root. The regions of outflow for the skeletal and visceral efferents were therefore in these cases both displaced together in the same direction and as far as one could judge to about the same extent.

For what amount of longitudinal extent of the cord the above general rule may hold good is deducible from the following observations.

In the arm just as in the leg there seems a *prefixed* type as well as a *postfixed* type of plexal innervation. When the innervation of the leg is of the high type, will the innervation of the arm be also of that type?

In nine experiments this point of relationship was examined. In two of the experiments the outflow of the motor fibres for the leg in the lumbo-sacral nerve-roots was of the more usual *postfixed* type (*e.g.* the 9th supplied the short flexors of the digits), in each of these two cases the 2nd thoracic root contained motor fibres for the long and short flexors of the fingers. Seven of the experiments were made when the outflow of the motor fibres for the leg was of the *prefixed* type (*e.g.* the 9th did not supply any muscle of the leg or foot). In three of these seven cases the 2nd thoracic contained the usual motor fibres to the intrinsic palmar muscles of the hand, in four excitation of the 2nd thoracic root gave besides flexion of the digits and pollex with adduction of the latter, a pronation and flexion of the wrist much more marked than is usual. The flexion of the digits and wrist persisted without obvious impairment after the ulnar nerve had been divided at the wrist, and in one instance in a partial way after the ulnar had been divided at the level of the olecranon process. In two specimens the flexor sublimis was thrown into strong contraction as well as was the deep flexor. In these cases the 2nd thoracic root sent in greater extent than usual motor fibres to the long flexors of the fingers, and the type of innervation was markedly low for the arm in an individual in which the type of innervation of the leg was exceptionally high. I examined by dissection the brachial and lumbo-sacral plexuses of ten Rhesus. In the specimens 4, 5, and 10 both plexuses were also tested physiologically and the lumbo-sacral found to be of the high type, and the brachial of the low type.

From the table it seems that the constitution of the lumbo-sacral plexus may be very different in individuals which do not exhibit obvious anatomical differences between the constitution of their brachial plexuses. In the cat and dog the brachial plexus is almost always of a kind that would in rat, rabbit and macaque be *prefixed,* that is, the 2nd thoracic root does not enter into it. Yet the sciatic plexus of the cat is sometimes of the postfixed, sometimes of the prefixed class, that is sometimes the 9th subthoracic root enters into it, sometimes it does not. The shiftings forward or backward in the brachial and pelvic regions appear independent one of another.

Again, as has been described in a special section of this paper, the knee-jerk is usually mainly dependent on the integrity of the root of the 5th lumbar-nerve, occasionally however it is as largely dependent on the 4th as on the 5th; in one instance of this kind on investigation the muscles of the foot were found not represented as low as the 9th root, only extending into the 8th. The representation of the extensors of the knee was extremely high, the representation of the short flexors of the digits unusually high in one and the same individual.

Without attempting to draw wide conclusions from experiments that should perhaps be much more numerous to securely warrant them, I

Specimen	Root	Lumbo-sacral Plexus.	Root	Brachial Plexus
1 L.	5th sub. thor. 9th ,,	to anterior crural < to lumbo-sacral cord filament to internal popliteal	5th cerv. 2nd thor.	fair branch to join 6th cerv. ,, ,, 1st thorac.
2 V. L.	5th sub. thor. 9th ,,	thread to ant. crural; trunk to lumbo-sac. cord filament to internal popliteal	5th cerv. 2nd thor.	good branch to join 6th cerv. small branch to join 1st thorac.
3 H.	5th sub. thor. 9th ,,	thread to lumbo-sacral cord; trunk to ant. cr. does not join the sciatic	5th cerv. 2nd thor.	small branch to join 6th cerv. good branch to join 1st thorac.
*4 H.	5th sub. thor. 9th ,,	thread to lumbo-sacral cord; trunk to ant. cr. does not join the sciatic	5th cerv. 2nd thor.	small branch to join 6th cerv. good branch to join 1st thorac.
*5 V. H.	5th sub. thor. 9th ,,	tiny thread to lumbo-sac. cord; trunk to ant. cr. does not join the sciatic	5th cerv. 2nd thor.	branch to 6th cerv. large as usual ,, 1st thor. is perhaps larger than usual
*6 H.	5th sub. thor. 9th ,,	thread to lumbo-sac. cord; trunk to ant. crural does not join the sciatic	5th cerv. 2nd thor.	fair branch to join 6th cerv. ,, ,, 1st thorac.
7 V. L.	5th sub. thor. 9th ,,	trunk to lumbo-sac. cord; a filament to ant. cr. filament to internal popliteal	5th cerv. 2nd thor.	good branch to join 6th cerv. small branch to join 1st thorac.
8 L.	5th sub. thor. 9th ,,	branch to lumbo-sac. cord > branch to ant. cr. filament to internal popliteal	5th cerv. 2nd thor.	fair branch to join 6th cerv. ,, ,, 1st thorac.
9 L.	5th sub. thor. 9th ,,	branch to lumbo-sac. cord > branch to ant. cr. filament to internal popliteal	5th cerv. 2nd thor.	fair branch to join 6th cerv. ,, ,, 1st thorac.
10 H.	5th sub. thor. 9th ,,	branch to lumbo-sac. cord < branch to ant. cr. no filament to the sciatic	5th cerv. 2nd thor.	small branch to join 6th cerv. good branch to join 1st thorac.

would nevertheless point out here certain facts met with in the variation of nerve-root constitution, and of limb-plexus construction.

As already said, the constitution of the nerve-roots in each of the species examined, Frog (R. temporaria), Rabbit, Cat, Macacus Rhesus, and Macacus (Bonnet), individual variation is so extremely frequent within a certain narrow range that it is difficult to say within that range what type predominates. The range allows of a displacement of origin of a root-filament sufficient to remove it from the upper to the lower half of the same root, or from the lower half of one nerve-root into the upper half of the next below. This range of oscillation is about the same in each of the species examined, and it is not greater or less in Macacus than in cat or rabbit. It is revealed by dissections as it is by physiological experiments, and, to judge by dissection, is present in man just as in Macacus and cat. By the displacement not one root-filament alone, nor all the filaments of one root alone, but all the root-filaments of several adjacent roots are affected together and in the same sense. But this is true only of one, usually considerable, region of the cord. In the lumbo-sacral region all the roots may be displaced downwards to an extreme degree and yet the brachial roots not be displaced, or the latter may be displaced upward. It is evident that this shifting amounting to about half the origin of a nerve-root is not, however else it may be explained, explicable by suppression or duplication of a root or a somite. The suppression of a root is perhaps not infrequent in the lumbar region of Macacus. One individual examined possessed six lumbar roots instead of seven, and six lumbar vertebræ instead of seven. But this suppression is relatively to the shift from postfixed to prefixed quite infrequent. Moreover suppression means condensation of the length of spinal origin; but in a *prefixed* plexus the length of spinal origin of the muscle-nerves is not necessarily less than in a *postfixed* plexus.

In none of the species used in my experiments have I found the extreme limits of individual variation involve so much as the whole length of a nerve-root as measured by the *larger* nerve-roots. Thus the upper limit for the intrinsic plantar muscles oscillates from the top of the 7th root to somewhat more than half-way up the 6th: the outflow for the soleus oscillates from the bottom of the 8th root to somewhat more than half-way up it. The pronator quadratus from a third of the way up the 2nd thoracic root to as high as the lower border of the 1st thoracic. And with regard to the nature of the variation the induction made by Herringham[1] that although any given fibre may alter its

[1] *Proc. Roy. Soc., loc. cit.*

position relative to the vertebral column it will maintain its position relative to other fibres has always held true. A slight restriction in this law, viz. the restriction of its application to the region of one plexus, does it is true appear needful, because with upward shifting of the lumbo-sacral plexus there may coexist, as I have shewn, no shifting, or even a downward shifting of the brachial plexus. So that the relative position of the fibres of the two plexuses taken together does not remain exactly the same as before.

When the upper limit of the outflow of motor fibres to the intrinsic plantar muscles does not extend into the 6th root at all, the lower limit of outflow is in the 9th root. It is easy with care to divide the 9th root into three bundles in axial series, but the lower origin of the fibres for the plantar intrinsics, if in the 9th at all, extended into the third filament in three experiments in which I split the nerve thus. That is to say, the amount of shifting which lifts or depresses the limit of a region of outflow through a fraction of a large root with a long region of spinal origin suffices in the same individual to move the lower limit through an entire nerve-root which has a short region of spinal origin. This looks as if the whole region of outflow for a muscle were shifted bodily a certain distance, for instance, a couple of millimeters, irrespective of nerve-roots. The region of surface origin of the 6th root measures 8 mm. in a large Rhesus, the region of surface origin of the 9th measures barely 3 mm. If then the upper limit of origin of the outflow for a muscle move through the same distance as the lower limit of its origin, one limit may be shifted through a small fraction of the region of origin of a large root, while at the same time the other limit may be shifted through a large fraction of the region of origin of a small root down in the conus medullaris. This seems to point to the minor variations so constantly affecting the composition of the nerve-roots not being phenomena of the same class as the alterations less frequently occurring in the actual number of the nerve-roots of a region, where suppression or addition of a root has taken place.

The suppression or duplication of a spinal root which goes with suppression or duplication in the vertebræ sometimes bridges over the normal difference between species and species, but sometimes it does not. It might be thought, as the lumbocrural roots of Macacus differ from those of dog merely in their being reduced in number by one root, and would if themselves reduced by one resemble those of man, that the three types formed a consecutive series, and that when as a variety in Macacus the lumbocrural roots were reduced to the number typical in man, the root-composition of the plexus would resemble that of man, as it would do were the suppressed root one of the upper two. Yet in one of the above specimens of the variation such was not the fact, as may be seen from the figure given. The plexus resembled in its upper part a normal one of the prefixed class; the anterior crural came from the 4th, 5th, and 3rd roots, the fourth contributing a larger bulk to the crural than did the 5th; the external cutaneous came from the 3rd and 4th; the sciatic received a good branch from the 5th. But the sciatic had only 3 roots instead of four; the lowest lumbar root seemed to represent the two lowest lumbar of the usual arrangement. The physiological examination of this plexus made of course previous to the anatomical yielded results only explicable on that view. Thus for instance the Flexor longus hallucis was thrown into contraction by the lowest two lumbar roots only (in this case the 5th and 6th subthoracic), and chiefly by the lower of the two. The soleus was thrown into action by the lowest lumbar and the highest sacral roots, only, namely, by two roots only, and these in this specimen the 6th and 7th subthoracic. The semimembranosus was also innervated by two roots only, the 6th and 7th subthoracic. The intrinsic flexors of the digits were supplied by the same two roots only. The 8th subthoracic of this case did not innervate the limb muscles at all, but it caused contraction of the anus, and, as judged by inspection, unmistakable contraction of the urinary bladder.

It must be admitted however that the variability in the anatomical and physiological composition of the spinal nerve-roots is not described by some authorities (Remak, Ferrier and Yeo, Bert and Marcacci, Knie) and has by some been denied[1]. Krause says of the abnormalities of limb nerves that they affect only the course of the fibres from the centres to the periphery, the terminations themselves, central and peripheral, remaining invariable. Henle also wrote, "It is precisely with regard to the central and peripheral points which any nerve-fibre connects together that the greatest constancy (Beständigkeit) exists. But between its end points it can move with greater freedom and take this route or that—in view of which fact becomes clear the significance or rather insignificance of nerve-variations." But is the variation in the peripheral nerve-trunks, frequent though it be, more frequent than or so frequent as the variation in the spinal roots entering those trunks?

[1] Apparently by Dr R. Russell (Prof. Horsley's laboratory) in the *Proceed. of the Roy. Soc.* March, 1892, appearing when this was in the press.

The variation in the root-composition of the nerve-trunks of the plexus does not seem to entail at all, or to be at all associated with, difference in the behaviour of the nerve-trunk when once composed: I have made dissections for comparison of the distribution of the anterior crural nerve when arising from a low plexus and when arising from a high plexus; I fail to discover any obvious difference in the distribution of the nerve in the two cases. I have dissected the obturator, the anterior tibial, the posterior tibial and the musculo-cutaneous nerves in the same way from high and low plexuses, and have failed to discover obvious differences between them. An anterior crural nerve-trunk formed chiefly from the 5th subthoracic spinal root with a subsidiary contribution from the 4th and a fine filament from the 6th, exhibited to dissection a distribution quite similar to that of an anterior crural composed mainly from the 4th root with subsidiary contributions from the 5th and 3rd. It would seem that the plexus trunks are more stable anatomical entities than are the nerve-roots. In saying so it must be remembered that one makes the assumption that the muscles are in the compared cases comparable, i.e. that for instance the tibialis anticus muscle in one individual is really the same thing as the tibialis anticus of another individual, two cases being taken of course where there is no obvious difference between these muscles. This not exorbitant assumption being granted and the muscles being taken as landmarks, the peripheral nerve-trunk is found to be more constant than is the spinal nerve-root.

Even in the case of the complete suppression together of a lumbar vertebræ and of a spinal root, as already described, dissection revealed no obvious difference in the branching or distribution of the very nerve-trunks that were most affected by the absence of the absent root. The vertebræ and root suppressed were either the 6th or the 7th lumbar, that is to say, the lowest root of the lumbar series did duty for both; although large, it was not extraordinarily so. The motor branches of the anterior tibial and of the posterior tibial in the leg were carefully dissected and compared with the ordinary type already shewn to be common to both high and low types of plexus-formation and found not to differ obviously from them. The branching from the n. musculo-cutaneus to the peronei and the branchings of the hamstring nerve were also compared and no obvious difference found.

The afferent nerve-trunks and the mixed sensorimotor appear to undergo variation in their root-composition together, at least in many instances. When the anterior crural was of postfixed composition I have seen the external cutaneous receive a branch from the 5th root as well as from the 4th and 3rd. In the frog however the afferent trunks may be of *prefixed* composition in the same plexus in which the efferent are not of *prefixed* composition.

In face of the constant oscillation of root origin it becomes obvious that in any particular instance of muscle and spinal nerve-root connection either the spinal nerve-root may be put foremost and considered an example of, let us say, the high, anterior, or prefixed type of its distribution, or in the same instance the muscle may be put foremost and described as being an example of its low, posterior, or postfixed type. But because the trunks and branches of the plexus, together with the muscles and other peripheral organs to which the nerve-trunks are attached, seem to form a stable and relatively fixed annex, tied to the central nervous system by connections the exact point of attachment of which to the cord varies within a certain range so frequently that it is difficult within that range to consider any one point more normal than another, it seems preferable to place the muscles and plexus-branches foremost and to say they offer two classes of nerve supply, a low, posterior or postfixed class, and a high, anterior or prefixed class, according as the constituent nerve-fibres come from in front of or from behind a mid-point of the range of variation. In the same way the type of plexus has in this paper been styled prefixed or postfixed, in reference to the root-fibres proceeding to it arising mainly in front of or from behind the mean point of oscillation of the region of origin of the plexus from the cord. In speaking of a mean point about which the region of origin seems to oscillate it is not intended to infer that instances of origin of the plexus from the mid point of the region are more frequent than from elsewhere in the region, but the mean point is only taken as a convenient expression of the position of the region. It may be that the mid point is also the point of greatest frequency of occurrence, but it might require some hundreds of determinations to shew that fact.

In comparing the plexus of one species with the plexus of another species the exceptional cases where suppression or addition of a segment has occurred would naturally not be selected as representing the normal; but, as has been shewn, the normal itself contains classes, and in comparing rabbit or cat with Macacus the prefixed class of the former should not be compared with the postfixed class of the latter, but the prefixed with the prefixed, and the postfixed with the postfixed. If this be done there is a fair field given for observing whether in Macacus rhesus there is any hint in the construction of the lumbo-sacral plexus of the far greater and more complete musculature and movement of the hind foot of Macacus as compared on those points with the hind foot of rabbit and cat. A difference becomes evident at once. The root-composition of the anterior crural nerves is not obviously different in the two animals if it be remembered that the "normal" cat has an extra segment in the upper part of the lumbar region which Macacus has not. The anterior crural in cat and Rhesus compare together thus:

	Cat	Rabbit	Macacus Rhesus
Prefixed normal type	4 **5** 6	4 **5** 6	3 **4** 5
Postfixed normal type	4 5 **6** (7)	5 **6** 7	3 4 **5** (6)

The obturator is also not obviously different in the two; thus:

	Cat	Rabbit	Rhesus
Prefixed normal type	4 **5** 6	4 **5** **6**	3 4 5
Postfixed normal type	4 5 **6** (7)	**5** **6** 7	3 4 **5** (6)

(In each case the nerve-root which contributes the main share to the plexus-nerve is shewn by its number being in thick type.)

On comparing the root-composition of the sciatic an obvious difference appears.

Great Sciatic	Cat	Rabbit	Rhesus
Prefixed normal type	**6** **7** 8	6 **7** **8**	**5** **6** **7** 8
Postfixed normal type	6 **7** **8** 9	6 **7** **8** 9	5 **6** **7** **8** 9

It will be noticed that the sciatic of the monkey is richer than that of the rabbit or cat by the afflux to it of lower roots which in them it does not receive. The sciatic of Macacus is sometimes constituted by five roots, the sciatic of the cat and dog is never constituted by more than four. Sometimes it is true in Rhesus the 5th root does not contribute to the sciatic trunk at all.

How has the extra root entering into the composition of the sciatic of Rhesus been obtained? Has it resulted from duplication of one of the roots contributing to the sciatic in a simpler form of plexus such as that of cat and dog? Or has it been obtained by the addition to the sciatic of a nerve-root which did not previously contribute to the plexus. In the latter case the root added must have been added at the posterior end of the plexus, because the correspondence between the lumbar and highest sacral roots is of the same character throughout the plexus until the 9th subthoracic root is reached. 1st lumbar of Macacus is analogous to the 2nd of cat and dog, the 5th of Macacus to the 6th of cat and dog. But the 2nd sacral of Macacus corresponds to the 2nd sacral of cat and dog, and not merely as regards its distribution to the limb muscles (intrinsic plantars) but also as regards its distribution to the pelvic viscera (bladder, rectum) and the sphincters of the anus and the vagina. The 1st sacral of Macacus and the cat and dog also are strictly analogous in function; the correspondence between the distributions of it in the two types is quite remarkable; not only as to the limb muscles, but as to the anus and the bladder.

This looks as though the extra root in the sciatic of Macacus had not been brought into the sciatic by the addition to it of the root nearest behind those contributing already. It might perhaps be supposed that with the extraordinary development of the musculature of the foot in Macacque the region of outflow of efferent fibres to its muscles has increased, and that the greater space demanded by the increase had been found by an extension of the outflow region backwards into the precincts of the next segment behind it. But that argument offers no explanation for the shifting backward in Macacus of the representation of the anus and bladder in the efferent roots as well as of the representation of the most segmentally posterior of the limb-muscles as well.

One is therefore driven to the conclusion that the 7th subthoracic root of the cat and dog is physiologically equivalent to the 6th and 7th of Macacus, and that the analogous roots in the plexuses of the two types may be tabulated thus:

Man	Macacus	Cat (Dog)	Frog
	1st lumbar	2nd lumbar (? + 1st)	
1st	2nd „ (? + 1st)	3rd „	
2nd	3rd „	4th „	7th spinal nerve
3rd	4th „	5th „	7th spinal nerve
4th	5th „	6th „	7th spinal nerve
5th	6th „	7th „	8th spinal nerve
6th (1st sac.)	7th „	7th „	8th spinal nerve
7th (2nd sac.)	8th „ (1st sac.)	8th „ (1st sac.)	9th spinal nerve
8th (3rd sac.)	9th „ (2nd „)	9th „ (2nd „)	
	10th „ (3rd „)	10th „ (3rd „)	

It will be remembered that the one instance of condensed formation of the plexus met with in the series of seventy examined, was an example in which the 6th lumbar root did duty for the 6th and 7th usually present, there existing in that instance no 7th root at all. On the explanation just offered that exceptional instance might be perhaps considered a case of reversion to the more simple plexus of an older type.

If now the rabbit's plexus be compared with that of cat and dog it is seen that no essential difference between them exists, although minor differences do. When the sciatic plexus of the frog is compared with the type exemplified by rabbit, cat or dog, it is too difficult to assign analogies but it nevertheless appears clear that in deduplication of the roots of the former the key to a comparison must lie.

Without attempting to enter at any length into questions concerning morphology of the mammalian limb, it seems desirable to inquire what is the general arrangement revealed by the distribution of its motor nerves.

The scheme arrived at by Peyer, Krause, and Schwalbe for the construction of the muscular mass of the limb makes it a compound of detached myomeres or portions of myomeres so piled one on another upon the long axis of the limb that the most segmentally posterior is apical. The free apex or distal end of the limb is formed out of a piece of a body-segment detached from the most posterior of those somites which contribute to the limb at all. The next or penultimate portion of the limb is a detached piece of the most posterior but one of the metameres contributing to the limb, and so on, until in the basal portion of the limb the metameres used are the most anterior and are not detached from the trunk portion.

Forgue and Lannegrace without making any induction content themselves with a statement that the roots that pass farthest into the member occupy the lowest position in the cord, a fact well illustrated by the prior experiments of Ferrier and Yeo.

Herringham[1] from analysis of the results he obtained by minute dissection of the human brachial plexus formulated certain "laws." Thus, "Of two muscles or of two parts of a muscle that which is nearer the head end of the body tends to be supplied by the higher, that which is nearer to the tail end by the lower nerve. Of two muscles that nearer the long axis of the body tends to be supplied by the higher, that which is nearer the periphery by the lower nerve." Of these conclusions the second when tested in the lower limb does not appear to apply to the musculature of the posterior aspect of the leg and thigh.

Paterson[2] has studied the development of the limb plexuses and has shewn that each inferior primary division of a nerve-root separates again

[1] *Loc. cit.*

[2] *Journ. of Anat. and Phys.*, Vol. XXI. 611, and *Studies from the Owens College Laboratory*, 1891.

into a ventral and dorsal division; and that where the inferior primary divisions form limb plexuses the same separation into ventral and dorsal trunks can be found, and that these enter into the formation of the plexus, dorsal divisions uniting with dorsal divisions, ventral with ventral divisions, to form the great limb nerves. Thus in the lumbo-sacral plexus he points out that the obturator nerve results from fusion of ventral trunks, the anterior crural from a fusion of dorsal trunks. This view harmonises well with the results of excitation; thus when using weak excitation of a filament of the 4th root a pair only of muscles are thrown into action, that pair tends to be rectus femoris and upper part of gracilis; applied to a filament in the 5th root again if a pair be brought into action it tends to be vastus externus, and lower part of gracilis, shewing the equal footing of the two sets in each spinal segment respectively just as would be expected were they simply dorsal and ventral correlatives belonging to the same body segment. They bear the same mutual relationship as in abdominal segments, the dorsal part of the obliquus externus and the rectus abdominis.

I cannot however agree with Paterson in his view that the internal and external popliteal nerves are quite similarly related one to another; as judged of by their supply to the musculature and by their cutaneous distribution (to be discussed in a future paper) they do not appear to meet all the requirements of that view. For instance excitation shews that the peroneus longus and the tibialis anticus stand in a similar relation one to another in the 6th root as the vastus externus and the gracilis in the 5th root. In similar relation in the 7th root stand respectively the external and internal heads of the gastrocnemius muscle. In similar relation in the 8th root the flexor brevis minimi digiti and the flexor brevis hallucis.

Examined in the hind limb the distribution of the motor nerves to the skeletal muscles of the limb points to the limb being composed of a number of rays placed at right angles to the longitudinal axis of the body and parallel with the long axis of the limb. The most posterior of these muscular rays are the longest ones, and the most anterior the shortest ones of the limb series.

The prominence of the limb from the body is of such a form that the anterior edge of the prominence is thrust out less abruptly than is the posterior. The posterior edge is occupied entirely by one muscular ray, the last or hindmost. Into the anterior edge enter a number of rays. Taking seven to be the number of rays in the hind limb of Rhesus along the whole length of the posterior border from the free distal end of the limb to its attached base, runs the seventh ray, while into the anterior border enters each of the most anterior five of them.

If by a ray be meant a continuous band of muscle passing from the body axis to the periphery it is not difficult to trace in the limb the rays belonging to the 3rd, 4th, 5th, 6th, 7th, and 8th subthoracic segments, and to see that of these the 7th and 8th penetrate to the free apex of the limb. The ray of the 9th segment is less easily traced in its continuity. The distal part of it is obvious enough, namely, the intrinsic plantar muscles, but in the thigh and leg its traces are often obscure, sometimes, I think, not demonstrable. Often however when the thigh and leg portions appear at first sight to be absent, they prove really discoverable by minute inspection of the exposed musculature of the posterior aspect of the thigh and upper calf. They are more easily discoverable in the rabbit than in the cat or Macacus, if I may judge from six experiments made on the rabbit. In the cat more frequently than in Macacus the thigh portion of the ray is obvious, but in the leg is hard to discover.

If each of the body segments contributing to the limb be divided into four parts, a proximal between the axis of the body and the hip, a crural between the hip and the knee, an anti-crural between knee and ankle, and a distal in the foot, the representation of the muscular ray of each may be tabulated as overleaf.

It is there seen that the quadrifid or quinquifid digital partition of the free end of the limb does not imply that respectively four or five segments are prolonged into the apex of the limb.

In the fore-limb it is easier than in the hind-limb to trace the existence of the most posterior of the muscular segments as a raylike band lying in the length of the limb, because of the strong component it contributes not merely to the musculature of the terminal bit of the limb (manus) but to the penultimate (antibrachium). This and the greater regularity with which the ray contributes to the limb are the most striking differences between 2nd thoracic root with regard to the musculature of the fore-limb and the 9th subthoracic root with regard to the hind-limb.

It is clear that broadly described the musculature of the limb is built up by successive contributions of segments, which reviewed in series passing from the segmentally anterior to the segmentally posterior first extend stepwise down the antero-internal muscle-mass of the thigh, occupying its whole width from the adductor magnus internally to the vastus externus externally, and including the whole of the latter muscle. That

Part of Limb.	10. Ray	9. Ray	8. Ray	7. Ray	6. Ray	5. Ray	4. Ray	3. Ray
Proximal	abductors of tail superior lateral sacrococcygeus	abductors of tail sup. lat. sac. coccyg. Glut. max. (part of) Obtur. int. (part of)	abd. of tail sup. lat. sac. sacrococc. Glut. max. and superior (in cat)	Pyriformis &c.	Pyriformis &c.	Psoas &c.	Psoas, iliacus	Iliopsoas
Crural		Glut. max. vastus longus (part of) Tensor fasciae latae (sometimes, especially in rabbit)	Hamstrings vastus longus (espec. in cat)	Postcrural muscles	Postcrural muscles	Precrural and adductor muscles	Precrural and adductors	
Anticrural		(Soleus sometimes)	Post tibial muscles	Post and pretibial muscles and peronei	Post and pretibial muscles and peronei	Pretibial		
Distal		Intrinsic muscles of foot (sometimes; always if any of the crural or anticrural portion of the ray be present)	Intrinsics	Intrinsics	sometimes			

after composing this region of the thigh they extend stepwise down the leg occupying the front of it from the inner surface of the tibia internally to behind the peroneal muscles externally so as to include the latter group; and in Rhesus more than half the circumference of the limb; the next step is on to the dorsum of the foot, occupying its whole width, and forming the short extensor but not the dorsal interossei. The length of the limb having thus been reached and occupied by in both Macacus and the cat and rabbit the successively longer and longer out-thrusts of four segments, a number of other segments, usually two in the cat and rabbit, usually three in Macacus, thrust out each a process which extends along the back of the process of the segment immediately anterior to it and throughout the whole length of the limb. These segments are so intimately fused in the plantar region that it is difficult to pick out from the rest any one muscle which shews more of this or that constituent. But in the leg and thigh it is less difficult to demonstrate, for in them it can be shewn that the more superficial muscles, the gastrocnemius, the soleus, the semitendinosus and the surface portion of the biceps belong to spinal segments more posterior than do the long flexors of the digits, the semimembranosus and the deeper part of the biceps. And the former groups are posterior to the latter. The gastrocnemius and soleus are supplied mainly from 7th and 8th roots, but the flexor perforans mainly from the 6th and 7th. The inner hamstrings in the cat are each supplied by the 8th, 7th and 6th roots, but the supply of the semitendinosus (the more superficial) is more from the 8th than is the supply of the semimembranosus, while the supply of the semimembranosus is more from the 6th than is the supply of the semitendinosus. Herringham's second "law" is thus not apparent in the musculature of the posterior aspect of the lower limb. It is deduced from dissections of the upper limb. In the forearm of Rhesus in three instances I have found the flexor sublimis well supplied by the most posterior root entering the limb plexus, the 2nd thoracic; that is, the superficial flexor had a very posterior root supply. The same root, supplied however in these cases the pronator quadratus, and the flexor profundus also.

LONDON, *May*, 1892.

Addendum. I much regret the omission in Section IV. of fuller reference to the excellent work of Homén (Ziegler's *Beitrage*, 1890, p. 304).

On p. 764 it should be added that Gotch and Horsley (*Phil. Trans.* Oct. 1891) comparing the main anatomical features of the lumbo-sacral plexuses of Cat and Rhesus give a conclusion somewhat other than that at which I have arrived.

EXPLANATION OF FIGURES.

Plate XX.

Figures 1, 2, and 3 sketched from the lumbo-sacral plexus of Macacus rhesus. Fig. 1, A plexus of the "postfixed" class; fig. 2, a plexus of the prefixed class; fig. 3, a plexus from individual possessing six instead of seven lumbar vertebræ.

Figures 4 and 5. Outlines of the cerebral hemisphere of Macacus rhesus shewing the cortical area for movements of the anus and the focus of its representation.

Figure 6. Cerebral hemisphere of Dog, shewing the area of cortex from which closure of the vaginal orifice can be elicited.

Plate XXI.

Figure 7. Connection between external saphenous nerve and external plantar in Macacus rhesus.

Figures 8 and 9. Schemata illustrating the distribution of the fibres of the motor roots of the lumbo-sacral nerves of Rhesus; fig. 8, in the "postfixed" class of the muscle-supply; fig. 9, in the "prefixed" class of muscle-supply.

Figure 10. Spinal cord; admixture of large and small ganglion cells in the *lateral horn* at the first thoracic segment. (From photo-micrograph by Mr E. C. Bousfield).

Figure 11. Spinal cord shewing same admixture; lower magnification.

Figure 12. Bundles of the anterior root of the 9th thoracic nerve four months after section of the cord between the 8th and 9th thoracic nerve-roots. (From a microphotograph taken by Mr E. C. Bousfield.)

Figure 13. Effects of division of the anterior roots of the right-hand 2nd and 3rd thoracic nerves. Sketched from nature by Mr M. H. Lapidge. "On the side of the section the pupil is small, the hair is flat, the palpebral

opening small, the conjunctiva watery, the lower lid somewhat baggy, the cheek somewhat puckered, the pinna slightly flushed and projecting from the side of the head."—Extract from protocol.

Figures 14 and 15. Simple contractions of the gastrocnemius (frog) registered from separate excitations of the spinal roots VIII and IX. (p. 709).

Plate XXII.

Contractions of the urinary bladder of the monkey. For description see text, p. 677.

Plate XXIII.

T.a. signifies tibialis anticus muscle. *P* peroneus muscle, *G* gastrocnemius muscle. → denotes the direction of the movement of the recording lever when the muscle contracts.

Figure 1. Reflex movement of Frog. Action of tibialis anticus and peroneus.

Figure 2. Spontaneous movement of Frog. Action of tibialis anticus and gastrocnemius muscles. (Reduced to one-half of trace.)

Figure 3. Contractions of gastrocnemius and tibialis anticus given by mechanical excitations of root viii. and then root ix. (Reduced to one-third of trace.)

Figure 4. Spontaneous movement at tarso-crural joint of frog. The line marked *repose* was given by the tarsus when at rest. When at rest the position maintained was nearer full extension than full flexion at the ankle-joint. Time marked in $\frac{1}{50}$th seconds as in fig. 5. (Reduced to one-half of trace.)

Figure 5. Similar spontaneous movements evoked after separate registration has been arranged for the gastrocnemius and tibialis anticus respectively. From same experiment as fig. 4 about 10′ later. (Reduced to one-half of trace.)

Figure 6. Reflex movement. Contractions of peroneus and gastrocnemius muscles. (Reduced to one-half of trace.)

Figure 7. Strychnia. Convulsions. Contractions of tibialis anticus and gastrocnemius. (Reduced to one-third of trace.)

Figure 8. Spontaneous movement. *Alternate* action of tibialis anticus and gastrocnemius.

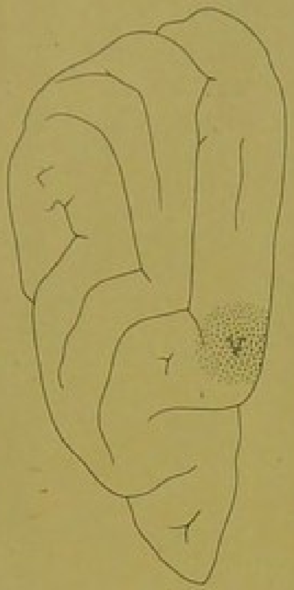
Figure 9. Reflex movement. Action of gastrocnemius unaccompanied by any activity of the pretibial muscles. The slight notch on the lower line was due to mechanical jar conveyed to the lower lever by sudden movement of the upper.

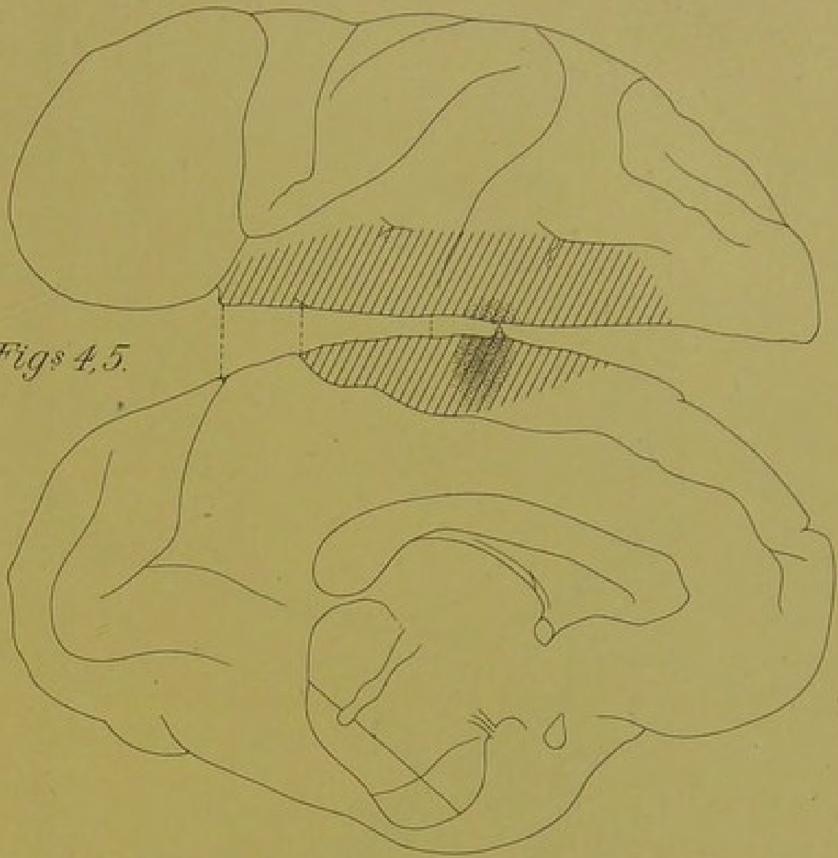
Figure 10. Reflex movement. Action of gastrocnemius and tibialis anticus. Time ·5″. (Reduced one-half from trace.)

Figure 11. Reflex movement; frog. *Alternate* action of gastrocnemius and tibialis anticus. Time ·5″. (Reduced to one-third of trace.)

Figure 12. Contractions of the gastrocnemius (frog) under separate excitations with 'break' shocks of the ixth and viiith spinal roots. Eight hundred and three contractions were registered from the ixth root, three from the viiith root. Of the contractions from the ixth root only three are reproduced in the figure. The fatigue effect is almost confined to contractions obtained from the ixth root. (Reduced to one-half of trace.)

Fig. 6.





Figs 4, 5.

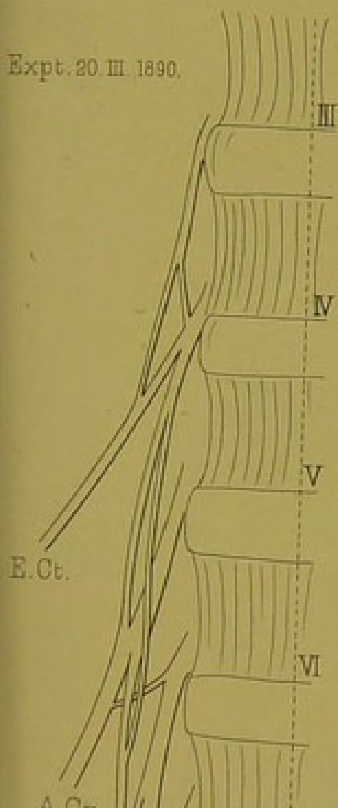


Fig. 1.

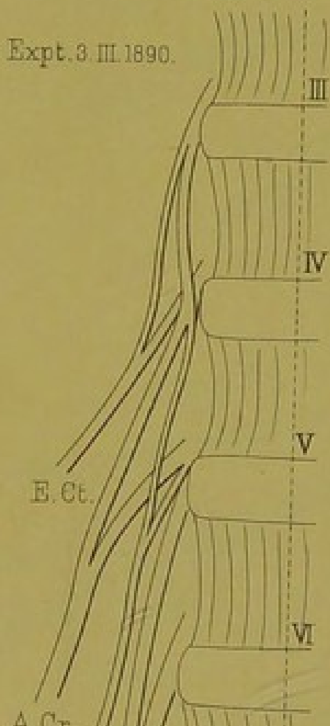


Fig. 2.

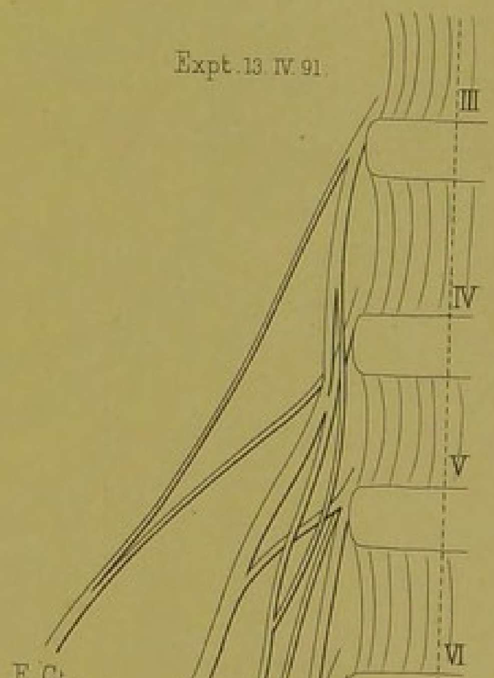


Fig. 3.

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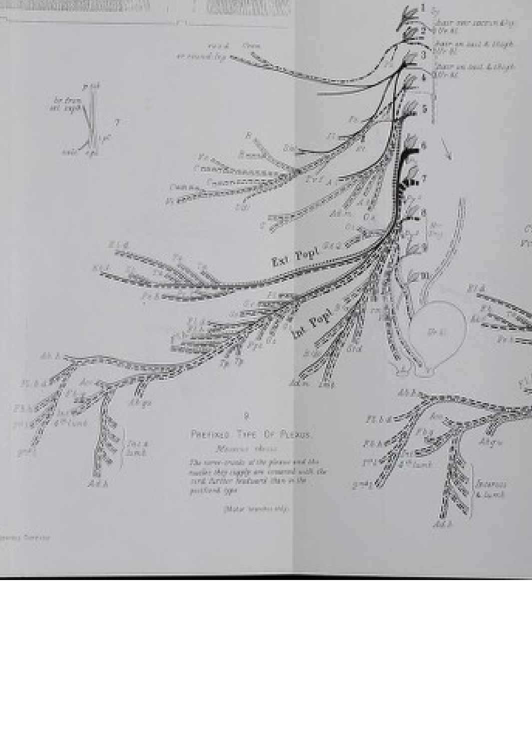

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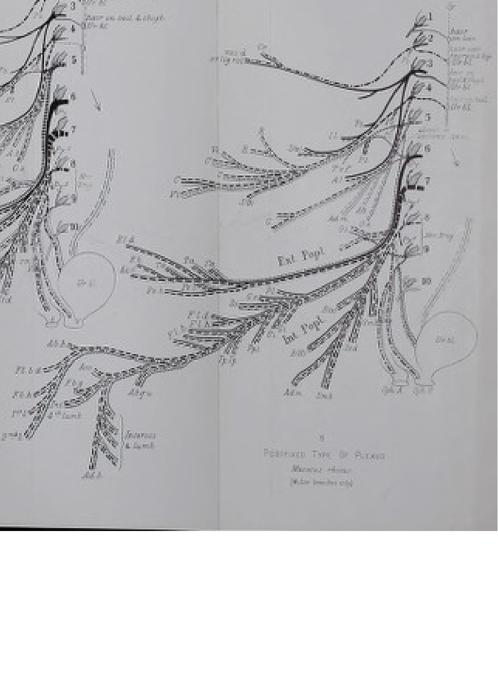
9

PREFIXED TYPE OF PLEXUS.

Macacus rhesus.

The nerve-trunks of the plexus and the muscles they supply are connected with the cord further headward than in the postfixed type.

(Motor branches only.)



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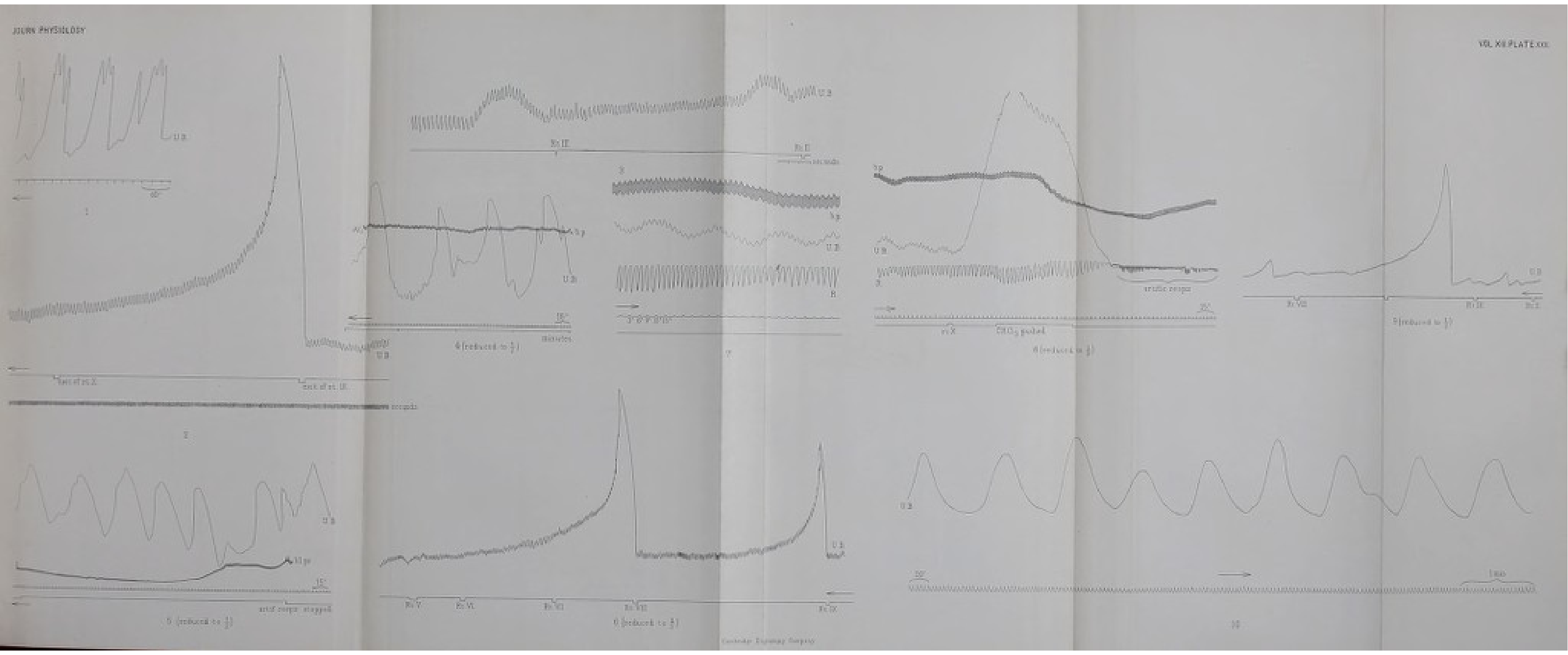
POSTFIXED TYPE OF PLEXUS.

Macacus rhesus.

(Motor branches only.)



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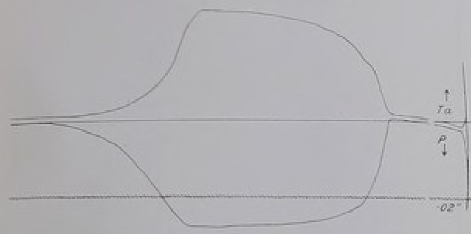

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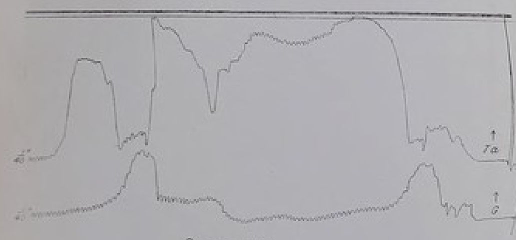

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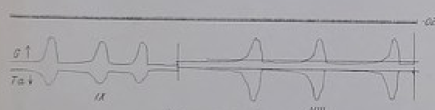

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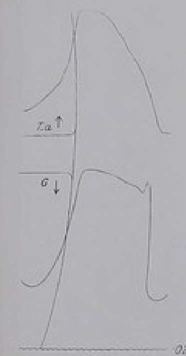

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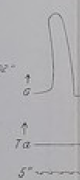

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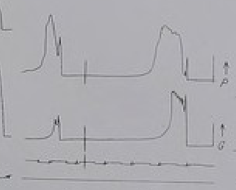

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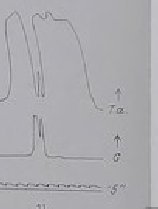

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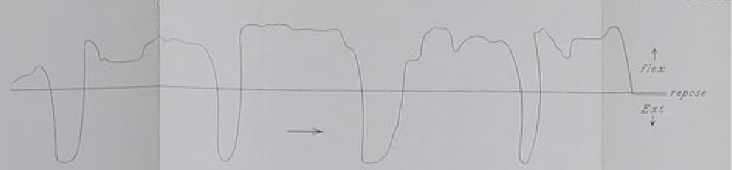

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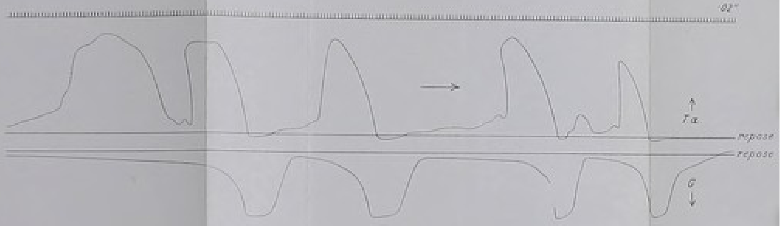

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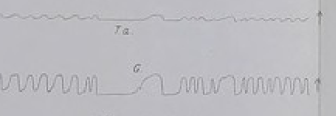

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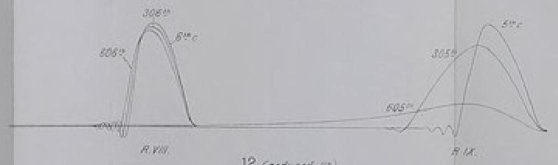

12 (reduced ½)

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