PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

# An Experimental Investigation of the Nerve Roots which Enter into the Formation of the Brachial Plexus of the Dog

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# II. *An Experimental Investigation of the Nerve Roots which enter into the Formation of the Brachial Plexus of the Dog.**

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(*From the Physiological Institute of Berlin and the Pathological Laboratory of University College, London.*)

[Plate 10.]

## Contents.



## I. Introduction.†

Numerous observers have from time to time endeavoured to determine the functional relationships between the nerve roots and the groups of muscles which they supply,

* Part of the expenses of this investigation have been defrayed by a grant from the Scientific Grants Committee of the British Medical Association.

† I wish to take this opportunity of expressing my most sincere thanks to Professor Gad, of Berlin, for his great kindness and courtesy in putting every facility in my way during the performance of the

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and the subject has been approached from various standpoints. Anatomists have long endeavoured, by minute dissections, to trace the relations which exist between the nerve roots and the various nerves derived from them, together with the muscles which these nerves supply. Such a minute dissection, aided by a process of maceration in dissociating liquids, was made by W. KRAUSE* in the case of the brachial plexus. Investigations of this kind established that each nerve root sends fibres to several nerves, and that each nerve receives fibres from several nerve roots; also, that the order of derivation from above down is constant, though the exact number of roots which supply any given nerve may vary.

SCHWALBE,† in a schematic representation of the human brachial plexus, shows the inferior primary divisions of the component nerves as dividing at their origins into dorsal, or posterior, and ventral, or anterior parts, and classifies the nerves of distribution to the arm into a dorsal and ventral set, the former derived from the dorsal divisions, and supplying the extensor surface of the limb, the latter from the ventral divisions, and supplying the flexor surface.

HERRINGHAM‡ made minute dissections of the human brachial plexus in fœtuses, stillborn children, and adults, in fifty-five instances, and traced the nerve fibres from the various roots through the plexus to the nerves, and in them to their final destination. From the results which he obtained, he was able to formulate the following laws:—

"Law I.—Any given fibre may alter its position relative to the vertebral column, but will maintain its position relative to other fibres."

"Law II.—A. 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."

"B. Of two muscles, that which is nearer the long axis of the body tends to be supplied by the higher, that which is nearer the periphery by the lower nerve."

"C. Of two muscles, that which is nearer the surface tends to be supplied by the higher, that which is further from it by the lower nerve."

earlier of these experiments, for the kind interest which he took in my work, and for his great willingness always to verify the results which I obtained from time to time. The original instrument devised to control certain movements of the limb while others were left free to take place, was made under his supervision, and almost entirely on the plan which he very kindly suggested. It is impossible for me to thank him warmly enough for the amount of trouble and personal inconvenience to which he put himself on my behalf.

To Professor VICTOR HORSLEY I owe a similar debt of gratitude, for allowing me to complete these investigations in the Pathological Laboratory of University College, and for his exceedingly kind and invaluable suggestions as to the general plan on which this paper should be arranged.

* KRAUSE, "Beiträge zur Neurologie der Oberen Extremität," 1865.

† SCHWALBE, "Lehrbuch der Neurologie," Erlangen, 1881, p. 914.

‡ HERRINGHAM, 'Proceedings of the Royal Society,' 1886, vol. 41, p. 423.

He also found that the sensory nerves obeyed the following rules :—

"A. Of two spots on the skin, that which is nearer the pre-axial border tends to be supplied by the higher nerve."

"B. Of two spots in the pre-axial area the lower tends to be supplied by the lower nerve, and of two spots in the post-axial area the lower tends to be supplied by the higher nerve."

PATERSON,* from dissections of the brachial plexus in the Porcupine, Koala, Rat, Rabbit, Guinea-pig, Cat, Camel, Brindled Gnu, Capucinus and Entellus Monkey, found that in five of these animals five nerves entered into the formation of the plexus; in four, four nerves gave rise to it; and in one (Entellus Monkey) six nerves were concerned in its formation. The nerves constantly present were the sixth, seventh, and eighth cervical, and the first dorsal; those not constant being the fourth, present in the Entellus Monkey, and the fifth, present in five cases. He was able to deduce the following conclusions from a comparison of the results by his dissections :—

1. The inferior primary divisions of the nerves entering the plexuses divide into dorsal and ventral trunks.

2. The dorsal divisions of the nerves always combine with dorsal divisions, the ventral divisions with ventral divisions to form the nerve of distribution.

3. The essential constitution of a nerve of distribution consequently never varies. A nerve arising from a combination of the dorsal divisions of certain nerves in one animal is never found in another animal to spring from the ventral divisions of these or any other nerves. The same rule applies to nerves derived from ventral divisions.

He further goes on to show that those parts of the limb derived from the dorsal surface of the embryonic limb, are supplied by nerves from the dorsal divisions, while those parts of the limb derived from the primitive ventral surfaces are supplied by nerves derived from the ventral divisions.

He suggests that in an early period of development the arrangement of the nerves is simple, supplying the bud representing the limb. The more pre-axial nerves are said to supply the pre-axial portion of the limb, the more post-axial the post-axial portion of the limb, while the inferior primary division of each nerve divides into a dorsal and ventral branch, to supply the dorsal and ventral surfaces of the embryonic limb. As the muscular system becomes developed and the changes take place in connection with the production of the adult condition, so the embryonic nerves are supposed to become more differentiated and complicated in their arrangement.

To ERB† is due the credit of having first recognised and drawn attention to the paralysis of a certain group of muscles depending on an affection of certain nerve roots. In all ERB'S cases the deltoid, biceps, and brachialis anticus were affected; in two in which it was examined, the supinator longus was also found affected, as was also the

* PATERSON, 'Studies in Anatomy,' Owens College, 1891, vol. 1, p. 135.

† ERB, "Ueber eine eigenthümliche Localisation von Lähmungen im Plexus brachialis." ('Verhandl. des Heidelb. naturhist.-med. Vereins,' N.S., 1, 2, 1874.)

supinator brevis. He ascribed the condition to an affection of the fifth and sixth cervical nerve roots; a conclusion which he afterwards verified by finding a motor point in the neck, stimulation of which produced contraction of the group of muscles he had formerly found paralyzed in combination.

Since ERB's publication, numerous similar instances have been recorded. A. KNIE* published a case in which the motor portion of the fifth cervical nerve root was divided during an operation. Immediately after the operation, the movements at the shoulder were unaffected, there was paralysis of the movements at the elbow joint, while those below the elbow remained normal. Exact differentiation of the muscles involved, however, was impossible, on account, apparently of diffuse changes.

A valuable series of cases of injury to the cervical region of the cord in Man at different levels, has been published by THORBURN,† which go to prove the relationship between the grouping of fibres in the nerve root and the respective levels of the spinal cord from which they are derived.‡

## II. HISTORICAL ACCOUNTS OF PREVIOUS EXPERIMENTAL RESEARCHES.

Experimental investigation in the lower animals is not only the most rapid, but also the most precise means at our disposal of ascertaining the functional motor relations of the nerve-roots. By this means our knowledge has been greatly increased, notably by the work of FERRIER and YEO in this country, and that of FORGUE in France.

MÜLLER§ and VAN DEEN,|| from experiments on the crural plexus of the Frog, together with a consideration of KRONENBERG'S experiments, to be afterwards referred to, came to the conclusion that, as far as the motor parts of the roots of the plexuses are concerned, the plexuses were arrangements for conveying fibres to each muscle from different parts of the brain and spinal cord, and that in them the sensory and motor fibres were possibly mixed to suit the wants of the areas which the nerves supply.

KRONENBERG¶ found that mechanical or electrical stimulation of each of the cervical roots which innervate the fore extremity of the Rabbit, resulted in nearly every muscle of the limb being thrown into contraction. His views as to the function of a plexus were identical with those of MÜLLER.

* KNIE, 'St. Petersburg Med. Woch.,' 1889, Nr. 24, p. 215.

† THORBURN, 'Brain,' January 1887 and October 1888.

‡ DUCHENNE had previously recognised a form of "obstetrical" paralysis in which the deltoid, infra-spinatus, biceps, and brachialis anticus were involved; and in addition several other cases of localized paralysis were recorded by him, but without any attempt to interpret any of them by the light of anatomical facts.

§ MÜLLER, 'Handbuch der Physiologie des Menschen,' vol. 2, 1834, p. 685.

|| VAN DEEN, 'De differentia et nexu inter nervos vitæ animalis et organismi,' Leyden, 1835.

¶ KRONENBERG, 'Plexuum Nerv. Struct. et Virt.,' Berol., 1836.

PANIZZA,* by section experiments on the crural plexus of Frogs and Goats, was led to the same conclusion. He found that the amount of weakness produced in an extremity depended on the number of roots divided, and that, in order to obtain complete paralysis, all the roots must be divided. He therefore concluded that each root was capable of keeping all the movements intact, and that the difference between the action of one and all the roots supplying an extremity was merely one of degree.

PEYER† exposed the muscles by dissection, and noted which contracted on stimulation of each cervical root in the Rabbit. The sensory distribution he ascertained by dividing all the roots with the exception of one, and then finding in which area cutaneous stimulation resulted in reflex movements. He found that the group of muscles supplied by each root was a complex one, and not a simple one such as that of flexors or extensors; further, that each muscle was supplied by more than one root as a rule. He also came to the conclusion that the sensory roots were distributed to the cutaneous surfaces overlying the muscles supplied by the corresponding motor root.

KRAUSE,‡ by his researches, confirmed more or less those of the last observer. His method of procedure was that of tracing degenerations consequent on division of a given root in the Rabbit, along the motor and sensory fibres. He once divided the sixth and seventh cervical roots in the Monkey, and found that no degeneration followed in the ulnar and median "sensory nerves" of the hand, and concluded, therefore, that they derived their supply from the eighth cervical and first dorsal.

FERRIER and YEO§ found that in the Monkey stimulation of the individual roots determined not only contraction of various muscles, but a group of muscles in synergic combination, the effect of which was to produce a highly co-ordinated movement, as REMAK had supposed must be the case in Man. From this they concluded that section of each motor root would determine paralysis of the corresponding combined movement, but not necessarily the individual muscles involved, for, as many of the muscles are innervated by more than one root, the amount of paralysis of any given muscle would depend on the degree of motor innervation by the root divided, and that, therefore, though weakened, they would be still capable of entering into other combinations.‖

BERT and MARCACCI¶ obtained results in Dogs and Cats which essentially agree with the observations of the last-named experimenters. But, inasmuch as these

* PANIZZA, 'Annali Universali di Medicina,' 1834.

† PEYER, 'Zeitschrift für Rationelle Med.,' N.F., vol. 4, 1854.

‡ KRAUSE, *loc. cit.*, and 'Anatomie des Kaninchens,' 1868, p. 247.

§ FERRIER and YEO, 'Proceedings of the Royal Society,' 1881, vol. 32, p. 12.

‖ I do not add the details of the muscles supplied by each root, as observed by FERRIER and YEO, inasmuch as their observations relate to the Monkey and not to the Dog.

¶ P. BERT and MARCACCI, 'Gazette Med. de Paris,' 1881, p. 512.

observations were made with regard to the lumbo-sacral plexus of these animals, a detailed account of the experiments is not called for here.

FORGUE,* from the results of his investigations in the Frog, Dog, and Monkey, formulated the following three laws:—

1. Each root supplies the two opposite surfaces of the limb, the anterior and the posterior.

2. As one approaches the dorsal roots, the muscular contractions evoked involve the inferior segments of the limb.

3. At the same time, the contractions progressively involve the muscular masses proceeding from the radial to the ulnar side of the limb. He also adds: "It is a secondary law that the superficial layers are supplied before the deep."

This observer stimulated the respective nerve roots, after exposing and dividing them in the neural canal, in order to obtain the combined effect produced by stimulation of the whole root, but for the exact observation of the individual muscles related to each root, he resorted to stimulation of the branches arising from the different nerve-roots. All the roots supplying the plexus were divided before any of them were stimulated, and every other care was taken to preclude the possibility of error from diffusion of the electric current by which the roots were stimulated. The muscles were exposed by dissection in order to allow of direct observations of them during their action. In this way he determined the following arrangement of muscles in connection with the various nerve-roots of the brachial plexus in the Dog.

* FORGUE, 'Distribution des Racines Motrices dans les Muscles des Membres,' Montpellier, 1883.



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| Anterior surface of limb. | Posterior surface of limb. |
|---|---|
| VI. Cervical nerve root | |
| Humero-mastoid | Supraspinatus |
| Subscapularis | Infraspinatus |
| Biceps | |
| Coraco-brachialis | |
| Brachialis anticus | |
| VII. Cervical nerve root | |
| Subscapularis | Supraspinatus |
| Biceps | Infraspinatus |
| Coraco-brachialis | Deltoid (scapulo-acromial) |
| Brachialis anticus | Teres major |
| Pronator teres | Latissimus dorsi |
| Palmaris longus | Serratus magnus |
| | Outer and inner heads of triceps |
| | Extensor carpi radialis |
| VIII. Cervical nerve root | |
| Pectoralis major | Teres major |
| Deltoid (clavicular) | Latissimus dorsi |
| Pronator teres | Serratus magnus |
| Palmaris longus | All three heads of triceps |
| Flexor sublimis and profundus | Extensor radialis |
| Flexor carpi ulnaris | Extensor communis |
| | Extensor ulnaris |
| | Abductor of the thumb |
| | Dorsal interossei |
| I. Dorsal nerve root | |
| Pectoralis | Long head of triceps |
| Deltoid (clavicular) | Extensor communis |
| Flexor sublimis and profundus | Extensor ulnaris |
| Flexor carpi ulnaris | Abductor of thumb |
| Palmar interossei | Dorsal interossei |
| Lumbricals | |
| II. Dorsal nerve root | |
| Palmar interossei | |
| Lumbricals | |

Forgue also divided certain nerve roots, and kept the animals alive to study the paralysis which would result; but his results were very unsatisfactory, and he could come to no conclusions from them. He attributes his failure to the implication of roots, other than that divided, in inflammatory cicatricial tissue, which led to more extensive paralysis than that due directly to division of any given nerve root.

## III. Anatomical Introduction.

*The Brachial Plexus in the Dog.*—Ellenberger and Baum* describe and figure the brachial plexus in the Dog as found from the four last cervical (V., VI., VII., and

* Ellenberger and Baum, "Systematische und topographische Anatomie des Hundes," Berlin, 1891, p. 542.

VIII.) and the first and second thoracic nerve roots. The fifth cervical root is said to only send a feeble branch to the phrenic nerve; the sixth forms the suprascapular nerve, and sends a branch to the phrenic; the seventh sends branches to the musculo-cutaneous, phrenic, the median and circumflex, and forms an infrascapular nerve, and an anterior thoracic nerve; the eighth also forms an infrascapular and a thoracic nerve, besides helping in the formation of the musculo-cutaneous, musculo-spiral, circumflex, ulnar, and median nerves. The first dorsal root is said to form the posterior thoracic nerve, and to send branches to the ulnar, median, and radial. With it a feeble branch from the second dorsal root is said to be united. In the diagram of the plexus, a cord connecting the sixth and seventh cervical nerve roots is figured.

CHAUVEAU and ARLOING* do not give a separate account of the brachial plexus of the Dog, but describe that of the Carnivora, and mention any special points in which the Dog's plexus departs from the general type. They state that the last four cervical nerve roots and the first dorsal nerve root enter into the formation of the brachial plexus of the Carnivora; but that the twig from the fifth cervical root is an insignificant one. The musculo-cutaneous nerve is said to be formed from the sixth and seventh cervical roots; the musculo-spiral in the Dog exclusively from the eighth root, afterwards receiving branches from the median, ulnar, and circumflex nerves. These authors do not state from which roots the median and ulnar nerves are derived, but mention the fact that the ulnar joins the median in the upper arm, and that the median receives a branch from the musculo-cutaneous just above the elbow joint.

FORGUE† describes and figures the brachial plexus of the Dog, as formed by the three last cervical and the first two dorsal nerve roots. In his description he applies the term "médian externe" to what we would call the musculo-cutaneous, which is said to be derived from the sixth and seventh cervical roots. What he calls the "médian interne" we know as the median, and is formed from the eighth cervical and the first dorsal roots, according to him. His radial corresponds to our musculo-spiral, which he states has its origin from the seventh and eighth cervical and the first dorsal nerve roots, while the ulnar is derived from the first dorsal root.

A comparison of these descriptions shows us that certain discrepancies exist in the observations of these authors, for while ELLENBERGER and BAUM describe the musculo-cutaneous nerve as receiving its fibres from the seventh and eighth cervical nerve roots, the other observers quoted describe it as being supplied by the sixth and seventh cervical roots. In like manner the musculo-spiral is said by CHAUVEAU and ARLOING to come from the eighth cervical nerve root exclusively, afterwards receiving branches from certain other nerves; ELLENBERGER and BAUM describe it as having its origin from the eighth cervical and first dorsal roots, while FORGUE adds the seventh cervical root to those already mentioned. The median nerve is formed from the seventh and eighth cervical and the first dorsal nerve roots, according to ELLENBERGER and BAUM,

* CHAUVEAU, "Anatomie Comparée des Animaux Domestiques," 1871, p. 811.

† FORGUE, *loc. cit.*, p. 44.

while FORGUE omits the seventh cervical root in his description of the origin of this nerve. ELLENBERGER and BAUM say that the ulnar nerve springs from the eighth cervical and first dorsal roots; FORGUE, on the other hand, describes it as coming solely from the first dorsal nerve root.

From numerous careful dissections in the Dog, I find the following arrangement to be the most constant, but variations, of course, occur.

A. *Nerves.*—Only the sixth, seventh, and eighth cervical, and the first, and a minute twig from the second, dorsal nerve roots enter into the formation of the brachial plexus of the Dog (Plate 10, see fig. 1). The twig from the fifth cervical which is mentioned by certain authors, I have been unable to find, and the results of stimulation of this root confirm, at any rate for motor fibres, this anatomical observation, as will be subsequently seen. This root supplies the humero-mastoid muscle and gives a branch to the phrenic, thus supplying the diaphragm.

The musculo-cutaneous nerve at its origin comes exclusively from the seventh cervical and sometimes receives supply from the sixth root by axillary junctions. It sends a branch to the median nerve just above the bend of the elbow. The circumflex nerve is derived from the seventh cervical nerve root. The musculo-spiral takes its origin from the two last cervical and the first dorsal roots, the median from the eighth cervical, and the ulnar from the first dorsal root. The median joins the ulnar in the upper part of its course, and then separates from it again; the junction is one in which the ulnar sends a bundle of fibres to the median, and the median a bundle to the ulnar.

It will be thus seen that my observations, while not absolutely coinciding with those of any individual previous observer, agree in certain points with the observations of all of them.

B. *Muscles.*—The flexor carpi ulnaris muscle derives its nerve supply from both the median and ulnar, thus differing from Man, in whom it derives the whole of its supply from the ulnar. Very little need be said with regard to the other muscles, the majority of those found in the Monkey and Man being more or less perfectly represented in the Dog, but the supinator longus is so rudimentary that it is almost invariably destroyed during the reflection of the skin of the forearm. There is only one muscle representing the two radial extensors of the wrist, but its tendon of insertion divides into two, one half corresponding in its point of insertion to that of the long radial extensor of Man, while the other to that of the short radial extensor.

Although further details of the arrangement of the muscles is not required, it is very necessary to draw attention to certain consequences of their actions. In studying the mechanism by which the movements are brought about at the various joints, I found that action of the deltoid produced, in addition to the movement at the shoulder, a passive extension at the elbow joint. This latter might be produced by the force of gravity, the forearm simply falling as the upper arm is raised; but on the other hand, it can be produced owing to the fact that the long head of the triceps is not long enough to allow the upper arm to be raised to the level of the shoulder without its pulling on the forearm, and thus producing extension at the elbow. A more remarkable effect, however, is that which resulted when traction was directly made on the triceps, for not only was extension at the elbow produced, but extension of the whole extremity including the digits, all the segments of the limb being thus brought into a straight line. The way in which this is produced is that the extensor carpi radialis passes over two joints, viz.: the elbow and wrist, and the muscle is not long enough to allow the elbow to be fully extended without its pulling on the metacarpal bones into which it is inserted, and thus producing extension of the wrist. In like manner, the extension of the toes is due to the fact that their extensors, which also pass over more than one joint, are too short to allow extension at the wrist without their pulling on the bones into which they are inserted.

GAD* relates an exactly similar experience in connection with the posterior extremity of the Frog. He found that by drawing on the ilio-psoas muscle, he produced not only flexion of the thigh on the abdomen, but also of the leg on the thigh, and dorsiflexion of the foot on the leg, in fact the extremity was placed exactly in the position of a frog about to jump. The cause of this was found to be the fact that the insufficient length of the ham-strings did not allow complete flexion at the hip without pulling on the leg, and thus producing flexion at the knee. Then as the tibialis anticus has its origin above the knee joint, dorsiflexion at the ankle followed as a necessary consequence, the tibialis anticus in its turn not being long enough to allow of such extreme flexion at the knee, without drawing on the foot. The importance of these observations becomes apparent when we consider the numerous fallacies which would result if these facts were not borne in mind when we observed the various movements produced by stimulation of any single nerve root. Stimulation of a root, in which extension of the elbow is represented, would also produce extension of the hand and fingers, whether the muscles moving these parts were truly represented in that root or not. If one muscle can directly or indirectly produce movements at so many joints, it is clear that we must first eliminate the indirect effects of the action of this muscle, before we can study the movements of these joints, as produced by the muscles which act directly on them. The omission of this small detail possibly accounts for PANIZZA's conclusion that it was necessary to divide every root supplying an extremity before he could produce complete paralysis of any single movement.

An instrument was devised as follows, by means of which fixation at the elbow joint was obtained, without interfering with the play of the muscles acting on the wrist and digits (Plate 10, see fig. 2). The elbow was first flexed at an angle such as would place the extensors and flexors of the forearm as nearly as possible at an equal

* GAD, "Einige Beziehungen zwischen Nerv, Muskel und Centrum," DU BOIS-REYMOND's Archiv, 1880, p. 563.

advantage. The fixation was next obtained by an instrument consisting of two metal rods, one of which, as shown in the figure, was screwed into the head of the humerus, while the other, which had a clamp at one end, was fixed to one of the bones of the forearm; a rectangular rod was interposed between these rods, and one of its arms fixed to that which was screwed into the humerus, while the other was fixed to that connected with one of the bones of the forearm. These connections were brought about by means of double joints, so that the different rods could be fixed in any position with regard to each other, and thus the angle of the elbow could be varied to almost any degree necessary. The point of fixation of the rod connected with one of the bones of the forearm, was a point an inch to an inch and a half above the wrist joint. When pronation and supination were also to be excluded, this arm of the instrument was attached to the radius, otherwise it was, of course, usually fixed to the ulna. A rod fixed to some part of this instrument served to connect it to an iron upright screwed into the table; fixation being brought about in each instance by means of a double joint. This served to eliminate the movements at the shoulder also, and thus to give a still better opportunity of studying the movements at the wrist and digital joints pure and simple.

## IV. Operative Procedure.

*Operation.*—In every experiment the animal was narcotized with ether, either alone, or in combination with the subcutaneous injection of morphia. The animal was kept deeply under the influence of the narcotic during the whole of the experiment, and killed by an overdose of it at the end, except in the experiments in which the animals were allowed to live for a week or two, for the study of the degenerations which followed the division of nerve roots. In these latter cases the operation, which was always a very trivial one, was done under strict antiseptic precautions, and the small wound afterwards dressed antiseptically. The animals were of course narcotized in these, as in the other class of experiments.

The nerve roots were exposed in the neck, and traced to their points of exit from the intervertebral foramina. Two ligatures were passed round each root, the one as near to the vertebral column as possible, and the other a few millimetres distally from the first, and the root was then divided between the two ligatures. The same number of knots were made on each corresponding pair of ligatures, so that they could be compared when the dissection was made afterwards.

*Post-mortem.*—In every case a dissection was made so as to exclude the possibility of one nerve root being mistaken for another during the operation. The proximal ligature served a useful purpose, as without it one had to contend with troublesome hæmorrhage from branches of the intervertebral artery accompanying the nerve-root.

*Excitation.*—The distal portion of the divided root was then raised in the air and stimulated by means of fine platinum electrodes attached to the secondary coil of a DU BOIS-REYMOND'S inductorium supplied by a Daniell cell. Exactly the same apparatus was used in excitation of the cortex cerebri (*vide infra*).

## V. DIVISION OF SUBJECT AND ANALYSIS OF RESULTS.

### A. *Division of the Subject.*

In the following research I naturally approached the question by simple excitation of the peripheral end of the cut root, and the observation of the compound movement thus produced forms the first part of the investigation.

The next step was to carry out, if possible, a minute analysis of this combined movement dividing it into its component factors, *e.g.*, by using minimal currents of excitation applied to the separate bundles of nerve fibres in the nerve root. The strength of current necessary to produce the maximum effect, without diffusing to other nerve roots was found, on the average, to be that in which the secondary was 15 centims. distant from the primary coil. Every care was taken to avoid the possibility of errors from the diffusion of the current to other nerve roots. On using minimum strengths of current, secondary 25 centims. distant from primary coil, on the average, I found first that it was actually possible to obtain different movements by placing the electrodes on different points of the circumference* of the nerve root. I further noticed that on stimulating on one side of one of the small blood-vessels that could be seen with the naked eye running along the surface of the nerve root, a different movement was obtained to that evoked by stimulating the part of the root on the other side of such a vessel. Further, as is well known, the surface of the transverse section of a nerve root presents distinct divisions into bundles. It therefore seemed not unlikely that each bundle of fibres represented a different movement, and that with a little care it might be possible to divide the nerve roots longitudinally, and to separate the different bundles, and thus differentiate the representation of one movement from that of another. Accordingly using the small vessels before mentioned as guides wherever they existed, I divided each nerve root longitudinally into several different bundles, and found that by stimulating each bundle separately a different movement was obtained. These bundles corresponded to the natural bundles of which any given nerve root was composed.

This minute differentiation forms, therefore, the second part of the investigation.

Thus far the investigation dealt with movements. It was obviously necessary to pursue the matter further, and to see upon dissection what individual muscles were innervated by the various roots or their parts when successively excited. This forms the third part of the work. As a corollary to this latter question, I have attempted to determine to what degree any given root supplies a muscle when the latter is inner-

* BEEVOR and HORSLEY, 'Roy. Soc. Proc.,' 1888.

vated from several roots, and whether any given muscle is possibly supplied from more than one root. The instituting new experiments in control of the results obtained by the foregoing methods led to the planning of the following procedures.

Of these, the first, constituting the fourth part of the investigation, consisted in dividing one root, and then seeing what effect was produced thereby in the direction of alteration in the natural gait or movement of the fore-limb in progression.

Another control method, the results of which are embodied in the fifth part, was devised as follows:—A nerve root was divided (in some cases two roots); general epilepsy was then induced by electrical excitation of the cortex, and the resulting deficient participation, in the fit, of the limb in relation with the divided root carefully observed.

Finally, in the sixth part are collected the results of degeneration consequent upon section of the root or roots some time before death.

## B. *Analysis of the Results.*

It will be more convenient and instructive to place together the results obtained in Parts I. and II. of the investigation. They are based on a large number of experiments, and, although variations were met with, the results which appeared to be the most constant are those given here.

*Part I. Compound Movements obtained by Excitation of the whole Nerve root.*
*Part II. Minute Differentiation obtained by Excitation of the Individual Bundles of the Nerve root.*

*Fifth Cervical Root.*

No movement whatever of any part of the extremity under observation, with the exception of the scapula being fixed to the trunk, and drawn slightly upwards.

*Sixth Cervical Root.*

Part I. Upper arm raised to the level of the shoulder, with the forearm at right angles to the upper arm, the limb being adducted to the trunk and the elbow rotated out.

Part II. (1)* Upper arm raised to the level of the shoulder.
(2) Adduction of the arm to the side of the trunk, with outward rotation of the elbow.
(3) Flexion at the elbow.

[* The small numbers in brackets denote each of the individual bundles into which the nerve root was separated. Only those bundles destined for supplying muscles of the extremity are noted, which accounts in part for so few bundles being mentioned in connection with some roots; but it must also be remembered that the roots vary in size, the sixth cervical, and especially the second dorsal, being much smaller than any of the other nerve roots which enter into the formation of the brachial plexus. February 3, 1893.]

*Seventh Cervical Root.*

Part I. Fore-arm flexed fully on upper arm, the wrist touching the shoulder, and the whole limb drawn across the front of the thorax towards the opposite side.

Part II. (1) Upper arm raised to the level of the shoulder.
(2) Abduction of the elbow from the trunk, with rotation of the elbow inwards, *i.e.*, turning of the fore-arm on to the trunk.
(3) Drawing of the limb across the front of the thorax.
(4) Retraction of the elbow.
(5) Flexion ,, ,,
(6) Extension ,, ,,
(7) Flexion ,, wrist.
(8) Extension ,, ,,
(9) Supination ,, forearm.

*Eighth Cervical Root.*

Part I. The whole limb extended straight down by the side of the trunk, parallel to its long axis and in a straight line, with the digits very slightly separated.

Part II. (1) Arm drawn to the side of the trunk with tilting of the elbow outwards.
(2) Arm drawn down from the shoulder and fixed to the side.
(3) Arm drawn across the thorax to the opposite side.
(4) Arm drawn to the same side of the thorax.
(5) Retraction of the elbow.
(6) Extension ,, ,,
(7) Flexion ,, wrist.
(8) Extension ,, ,,
(9) Supination ,, forearm.
(10) Pronation ,, ,,
(11) Flexion ,, digits.
(12) Extension ,, ,,

*First Dorsal Root.*

Part I. The whole limb extended downwards obliquely across the same side of the abdomen, with the forearm pronated, slight ulnar flexion at the wrist, and wide separation of the digits.

Part II. (1) The arm drawn down and fixed to the side of the trunk.
(2) Extension of the elbow.
(3) Pronation of the forearm.
(4) Flexion of the digits.
(5) Extension ,,
(6) Abduction ,,
(7) Adduction ,,

*Second Dorsal Root.*

Part I. Digits separated and slightly flexed.

Part II. (1) Flexion (interosseal) of the digits.

(2) Abduction of the digits.

## *Part III. Direct Observation (after Dissection) of Muscles thrown into Action by Excitation of the Separate Nerve Roots.*

I next attempted to ascertain, as far as possible, which muscles are thrown into action by stimulation of the several nerve roots. The superficial muscles were exposed by removal of the skin and examined, while, with regard to the deep muscles, I frequently was able to examine them directly after the animal was killed, because the nerve roots at the end of a prolonged experiment retained their excitability for a considerable time, half-an-hour or more.

On account of the fact that no result among the muscles of the fore-limb followed excitation of the fifth cervical root, attention was only paid to the three lower cervical and the two upper dorsal roots with the following results :—

*Sixth Cervical Root—*

Brachio-mastoid.
Diaphragm.
Deltoid.
Supraspinatus.
Infraspinatus.
Subscapularis.
Coraco-brachialis.
Biceps.
Brachialis anticus.

*Seventh Cervical Root—*

Diaphragm.
Deltoid.
Supraspinatus.
Infraspinatus.
Subscapularis.
Teres.
Coraco-brachialis.
Biceps.
Brachialis anticus.
Triceps.
Flexors of the wrist.
Extensors of the wrist.
Supinator brevis.
Pectoralis.
Serratus magnus.

*Eighth Cervical Root—*

Pectoralis.
Teres.
Latissimus dorsi.
Triceps.
Flexors of the wrist.
Extensors of the wrist.
Supinator brevis.
Pronator teres.
Flexors of the digits.
Extensors of the digits.

*First Dorsal Root*—

Latissimus dorsi.
Triceps.
Pronator teres.
Flexors of the digits.
Extensors of the digits.
Interossei.

*Second Dorsal Root*—

Intrinsic muscles of the paw.

It is interesting to notice that, on the whole, the results obtained by me correspond to those obtained by FORGUE with a few exceptions, to which it may be well to call attention. With regard to the muscles supplied by the sixth root, there is only one point of difference. I find that the deltoid is supplied by this root, but FORGUE does not. The seventh root supplies the supinator brevis according to my observations, and not the latissimus dorsi and pronator teres as found by FORGUE, while he does not mention the supply of the supinator brevis at all in connection with any of the roots. The chief points of difference as to the muscles supplied by the eighth cervical root are that I do not find the deltoid and interossei thus supplied, while FORGUE does; and he does not mention the supinator brevis, while I find it to be supplied by this root. The representation of the deltoid and the omission of the pronator teres by FORGUE are the only points on which we differ with regard to the muscles deriving their nerve supply from the first dorsal root; and we are at one as to those muscles which depend on the second dorsal root for a like supply. Possibly the points of difference between FORGUE'S observations and my own are not so numerous as would appear from what has just been said, as his schematic representation, in order to show that each nerve root supplies muscles on both the anterior and posterior surface of the limb leads to slight confusion as to whether certain of the muscles are meant to be represented in certain roots; notably is this the case with regard to the deltoid, which I find it difficult to imagine as represented in the eighth cervical, much less the first dorsal nerve root.

*Corollary to Part III.*—The question which next arose for consideration was whether or no a single bundle of fibres representing a single simple movement ever remains distinct in a nerve root during its course to the muscles it supplies without inosculating with other nerve fibres. That each bundle does remain distinct is, I think, proved by the following facts:—

(*a*.) If a bundle of nerve fibres is separated in a nerve root, it can, in the Dog, be followed by dissection through the plexus and along the course of the nerve in which it runs, to its termination either in a muscle or in the skin.*

(*b*.) If a bundle thus isolated in a nerve root be stimulated a simple movement results and not merely the combined movement in only a lessened degree proportional to the diminished number of nerve fibres stimulated.

* *Cf.* HERRINGHAM, PATERSON, &c., *loc. cit.*

(*c.*) If a minimal stimulus be used one can localize different movements in different parts of the circumference of the peripheral nerve just as has been shown above to be possible in exciting a nerve root.

(*d.*) If the musculo-cutaneous be divided below the point where it gives off the twig to the median, and if the trunk of the nerve, above the point where the twig is given off, be stimulated, the pronator radii teres muscle contracts, and it alone. At first I was under the impression that the extensor carpi radialis was the muscle that contracted, but more careful separation of the two muscles by dissection showed that the movement in the latter muscle was due to traction on it owing to its connections with the adjacent pronator.

(*e.*) If a root be divided the degeneration which results in the various nerves receiving fibres from the root is not scattered but is limited to distinct strands sharply defined.

A further point to be determined in this connection was the question whether when a muscle receives nerve fibres from more than one cervical brachial nerve root, both nerve roots supply fibres to one and the same muscle fibre. The muscle chosen for these observations was the flexor carpi ulnaris, which, as we have already seen, is supplied both by the median and the ulnar trunks in the Dog. Now when the eighth cervical or first dorsal nerve root was stimulated alone, with a strong current, the maximum contraction of the flexor carpi ulnaris obtained was considerably less than that produced by stimulating both roots simultaneously. From this experiment it follows that the muscle fibres which are supplied by nerve fibres from one root in all probability do not receive nerve fibres from any other. This view is further supported by the experiment of GAD* on the lumbo-sacral roots of the Frog; for he showed that when a muscle is supplied by two nerve roots simultaneous stimulation of both roots produced an effect in the muscle equal to the sum of the contractions produced by stimulation of each root separately.

## *Part IV. (Control). Alteration in the Action of the Fore-limb in Progression or in Standing evoked by Section of a Nerve Root.*

The following experiments were performed to observe the effect of division of a nerve root on the movements by the limb during use in ordinary progression, &c. The four last cervical and the first dorsal nerve roots were each in turn divided in different animals under antiseptic precautions and a portion removed to prevent the possibility of reunion.

All the wounds healed by primary union except in one instance, and subsequent dissection in each case proved that none of the other roots were implicated in any of the cicatricial tissue. Each animal was kept under observation for a fortnight and then killed.

* GAD, *loc. cit.*

After division of the fifth nerve root alone absolutely no alteration could be observed in the mode of progression of the animal.

Division of the sixth root was followed by distinct paresis of the corresponding extremity, evidently chiefly implicating the muscles about the shoulder, the elbow tending to rotate away from the trunk when the animal walked; if the other fore leg were passively raised off the ground, the Dog had some difficulty in supporting the weight of the body on the leg, the nerve root of which had been divided, and in some cases failed to do so. In this as well as in the case of all the other nerve roots divided, this effect was most marked during the first twenty-four hours, after which it quickly passed off, so that in a day or two very little abnormality was noticeable, and by the end of a week it was difficult to say that there was any difference on the two sides. The effect of division of the seventh root resulted in a more extensive paresis, as it was evident that besides the slight tendency for the elbow to rotate away from the trunk on that side, there was some interference with the motor power of the lower segments of the limb, which made the lameness more noticeable than in the last instance. The most pronounced effect was that which followed division of the eighth cervical root, which is considerably the largest which enters into the formation of the brachial plexus in the Dog, the paresis being especially marked about the wrist, and the animal walking with a slightly high stepping action on the side of the divided root. Very little effect was produced by division of the first dorsal root, the resulting lameness being exceedingly slight and passing off very rapidly.

That reunion of the divided ends of the nerve roots was not the cause of the improvement in motor power which took place in each instance is proved by the fact that on post-mortem examination there was not the slightest sign of such reunion. Further, microscopic examination showed well-marked degeneration, both in the distal end of the roots divided, and in the nerves derived from these roots. As has already been shown, a muscle which obtains its nerve supply from several roots has some of its fibres innervated from one, while the remainder are innervated from another or other roots, so that the recovery cannot be explained by supposing that the same number of fibres are acted on as before, and that they gradually become accustomed to respond more powerfully to the stimulus, although that is necessarily less intense. At the end of three weeks the muscles supplied by the divided root were found to be considerably atrophied and softer than normal; and there was marked diminution of resistance when passive movements were carried out at these various joints on which these muscles acted. Moreover, during general epileptic convulsions artificially induced, these muscles did not stand out nearly so vigorously as did those on the non-affected side.

Division of the nerve root so near to the spinal cord may be supposed to have produced an amount of shock sufficient to render that part of the cord functionally inactive, or rather, reduced in its power of conduction. But if this were the case, there would at least have been some sign of weakness in the opposite fore leg, and probably also in the hind legs.

The only other explanation which suggests itself to my mind as possible is one or other of the following. Possibly certain cortical cells give origin to fibres which run in different roots to the same muscle or others of similar function, and division of one of these nerve roots produces a reflex inhibitory effect* on the cortical cells from which its fibres are derived, so that the original motor paralysis is more pronounced than that actually depending on the cutting off of the impulses which formerly travelled along the root that is now divided; and that as the cortical cells recover from this inhibitory effect, so the motor power is restored up to a certain point, the residuum not recovered from depending directly on the loss of the impulses which formerly reached the muscles through the now divided root. On the other hand, it may be that the cortical cells are capable of discharging the same amount of energy as formerly, but that the impulses meet with a block owing to the division of the fibres along which they formerly passed. Gradually, however, the impulses are diverted, it may be through the anterior horn cells of the spinal cord along other channels, and thus in time the fibres of the muscle which are supplied by an intact root receive almost the same amount of stimulation as did the whole muscle formerly.

It is worthy of note that Forgue could come to no satisfactory conclusions from the results which he obtained by this method of experimentation. He always found that the amount of motor enfeeblement was out of all proportion to that which could possibly be produced by division of a single nerve root; and on examination he invariably found that nerve roots other than that divided were implicated in the mass of inflammatory cicatricial tissue which resulted as a consequence of the suppuration of the wounds, a complication which never gave any trouble in the present research, as all of the wounds healed by primary union except in one case.

## *Part V. (Control). Influence of Section of Root or Roots in excluding part of an Epileptic Spasm induced in the Limb by Cortical Excitation.*

In my next series of experiments I tried to see what information could be obtained as to the functional relations of the nerve roots to the muscles they supply, by the following method of experimentation:—A nerve root was first exposed, but not divided; the cranium was then opened *lege artis* over the excitable area on the same side as the exposed nerve root, in order to avoid the possibility of injuring the cortical centres (*i.e.*, opposite) corresponding to the limb deriving its supply from that root. General (*i.e.*, bilateral) epilepsy was then produced by stimulation of the exposed cortex with the induced current as above stated, and the positions of the two fore extremities were seen to be identical during the fit. The exposed root was next divided, general epilepsy again produced, and the positions of the two fore extremities

* *Cf.* Bubnoff and Heidenhain, 'Pflüger's Archiv.'

once more compared. The position assumed by the two fore extremities before interference with the root, and of the sound one after the root on the other was divided, was as follows:—In this case, *i.e.*, the normal condition, the elbow was drawn close to the side of the thorax, the fore-arm held at right angles to the upper arm, and projected straight forward by the side of the thorax, the fore-arm, wrist, and fingers being in a straight line. During the first stage of the seizure, *i.e.*, during the tonic spasm, the extremity was raised parallel to the neck, with the paw on a level with the side of the head.

If, now, the sixth cervical root were divided, the elbow, during the epileptic convulsions, projected from the side of the trunk notably more than on the sound side, and the forearm was thus inclined across the trunk somewhat, so as to form an acute angle with the side of the thorax. It (the fore-arm) was still held at right angles to the upper arm, and the fore-arm, wrist, and fingers were, as before, in a straight line. During the tonic stage, the extremity was never raised higher than the level of the shoulder. This experiment shows, in a striking manner, that the exclusion from the fit of the muscles supplied by the sixth cervical root, means a loss of the same movements (*i.e.*, chiefly shoulder) as those previously determined by direct excitation of the root itself.

After division of the seventh cervical root, the elbow was fixed closer to the side of the thorax than on the normal side, the fore-arm extended obliquely across the abdomen, this demonstrating clearly the exclusion chiefly of the flexors of the elbow. (See p. 52).

Similarly division of the eighth cervical root alone was, in contrast to what has just been said, attended by elevation of the shoulder and noteworthy flexion at the elbow during the epileptic convulsions. Moreover, flexion of the paw at the wrist and of the digits predominated over extension. During the epileptic convulsions that were produced in a fourth animal, after the first dorsal root had been divided the upper arm remained close to the side of the trunk, in the same position as on the unaffected side, but the fore-arm became strongly flexed at the elbow (*i.e.*, owing to exclusion of triceps extension), so as to be parallel with the side of the neck. The fore-arm and wrist were in a straight line, but the digits were flexed and adducted.

I next performed in different animals combined section of more than one root as follows:—

The sixth and seventh cervical roots were simultaneously divided on the same side. During the convulsions the whole extremity was strongly extended down the side of the abdomen, the wrist and digits slightly curved in flexion, and the digits separated.

When in another animal the seventh and eighth cervical roots on the same side were similarly divided, the arm was a little more raised at the shoulder than on the opposite intact side, the fore-arm flexed on the upper arm, but not nearly so strongly as when the eighth root alone was divided.* The paw was flexed at right angles to the fore-arm at the wrist, and the digits interosseally flexed in the characteristic claw-shaped position, viz., hyperextension of the first phalanx with flexion of the distal phalanx. In the next experiment the eighth cervical and first dorsal roots were severed on the same side. On evoking the generalized convulsions the fore-arm was strongly flexed on the upper arm, as when the first dorsal alone was cut. Marked tendency to drop wrist, owing to very feeble spasm of the extensor muscles, was noted, and the digits were but slightly adducted and fully flexed.

In the next case the sixth, seventh, and eighth cervical roots were divided on the same side, and in the fit the elbow was fully extended as in unopposed triceps action, and the digits were spasmodically fixed in the claw-shaped position.

The fifth cervical root was then divided in addition to the three just mentioned, but the position of the limb, during the epileptic convulsions, was not altered by this, confirming the statement made on p. 47 that the fifth cervical root takes no share in the motor representation of the plexus. When the seventh and eighth cervical and the first dorsal nerve roots were divided the limb was extended straight forward from the shoulder, the whole extremity being in a straight line projecting in front of the animal and not raised above the level of the shoulder. Finally all the nerve roots entering into the formation of the brachial plexus were then divided. During the epileptic convulsions the extremity under these circumstances remained intrinsically motionless, although the limb was passively shaken by the convulsive spasms of the rest of the body.

So far as I am aware, this is the first time that this method of experimentation in connection with the nerve roots has been employed. It will be well, therefore, to point out that it possesses the double advantage of being a means of checking the results of direct stimulation experiments, and affording us the power of ascertaining whether elimination of a root does or does not result in incoordination of the remaining combination of movements. A few moments consideration shows that the results of these experiments completely confirm those obtained by stimulating the individual nerve roots, for during an epileptic fit, when a nerve root is cut, the muscles that act feebly are only those which are brought into action by direct stimulation of the same nerve root. Further, we see that the impulses travelling along the undivided roots produce perfectly coordinated movements, so that the coordination of the movement produced by the remaining roots is not in the slightest degree affected by the elimination of any one of them. These experiments also make it clear that when the section of the root and the cortical excitation are made at the same time there cannot be overflow of nerve impulses through the spinal centres, at any rate to any great extent. That is to say, impulses which should reach the muscles through the nerve root that has been divided, do not under these circumstances reach them by other commissural channels.

* Because of course the seventh cervical root has also been divided. See p. 58.





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*Part VI. (Control). Differentiation of Parts of the Nerve Roots by the Degeneration Method.*

The last set of experiments which were performed may, for convenience, be termed degeneration experiments. In these certain nerve roots were divided under the influence of an anæsthetic, and with antiseptic precautions. The animal was in each instance allowed to live for three weeks, and then killed. In order to prevent tedious repetition, it will suffice to say that microscopic examination showed that these experiments confirmed the anatomical facts that had been previously ascertained, as degeneration following section of a root was found only in those nerves which had been shown to have their origin from it. For example, division of the sixth root was followed by degeneration in the musculo-cutaneous, thus proving that this nerve does receive fibres from the sixth root in some cases; so, too, the musculo-spiral, about the origin of which there are discrepancies in the statements of different observers, was found to have some of its fibres degenerated after division of the seventh root. Another point of interest in connection with this root was the degeneration found in the *median* nerve after division of the root in question. It will be remembered that stimulation of the seventh root produced contraction of the pronator radii teres muscle, and that it has been also shown that stimulation of the branch which the musculo-cutaneous nerve gives to the median just above the bend of the elbow results in contraction of that muscle, and it alone.

But, in addition to these facts confirmatory of the results obtained by stimulation, certain interesting points were observed, of which, however, I will only allude to one in the present paper.

According to the Wallerian law of degeneration, division of a nerve root immediately on the distal side of the intervertebral ganglion results in degeneration of its peripheral end, and of that alone, there being no degeneration of the proximal end. In addition to degeneration of the distal end, as the Wallerian law affirms, I found some degenerated fibres in the sensory root between the ganglion and the spinal cord, which points to the probability that there are some fibres which run through the intervertebral ganglion, without being connected with the cells of the same. These observations confirm the statements of JOSEPH,* whose experiments of division of the root between the ganglion and the cord showed the existence of such fibres, and which, therefore, must have their trophic centres elsewhere—in the cord. As in my experiments the roots were divided on the distal side of the ganglia, if the trophic centres for these fibres be situated in the spinal cord, the only way in which the explanation will hold good is by supposing that such fibres are recurrent, as CLAUDE BERNARD has suggested, and that they loop back in the plexus, at the junction of the motor and sensory roots.† The only other way that the degeneration of these fibres can be explained is by

* 'Archiv für Physiol.,' 1887, p. 296.

† That this latter position is not the case is proved by my observations.

supposing that certain fibres derive their trophic supply in some way from the periphery; but I know of no facts that support any such supposition.

## VI. Summary and Conclusion.

From the results of the various methods of experimentation already detailed, I feel that I am justified in coming to the following conclusions:—

### 1. *Stimulation Experiments.*

1. The compound movement obtained by stimulation of a whole nerve root is a well coordinated one, depending on the action of a group of muscles in synergic combination, as Ferrier and Yeo* showed to be the case in the Monkey.

2. This compound effect may be resolved into its component factors, when it is found that movements diametrically opposed to each other may be represented in the same nerve root, *e.g.*, flexion and extension.

3. Such single simple movements bear an almost constant relation to the nerve roots, the same movements being as a rule found in any given root, and such movements always bear the same relation to the spinal level, *e.g.*, flexion of the elbow is always represented one root higher than extension of the same joint.

4. Fibres representing a certain movement as a rule preserve the same position in a given nerve root, *e.g.*, extension of the wrist is represented by a bundle of fibres in the upper part of the circumference, while flexion is represented by a bundle of fibres in the lower part of the same root.

5. Each bundle of nerve fibres, representing a single simple movement in a nerve root, remains distinct in its course to the muscle or muscles producing such a movement, without inosculating with other motor nerve fibres.

6. The group of muscles supplied by any given nerve root occupy both the anterior and posterior surfaces of the limb,† in other words, muscles whose unimpeded action would produce one movement, are represented in the same root as others whose action would produce a movement diametrically opposite.

7. In such combinations, certain muscles are always more extensively represented than others, so that with a current sufficiently strong to stimulate all the fibres in a nerve root equally, certain muscles predominate in their action over others.

8. The muscles whose action predominates in one root, always predominate in that root.

9. If the muscles producing flexion of a certain joint predominate in their action in one root, those producing extension predominate in another.

* *Loc. cit.*

† *Cf.* Patterson, Forgue, &c., *loc. cit.*


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10. It is possible by stimulation of a single bundle of fibres in a nerve root, to produce contraction of a single muscle and it alone.

11. The same muscle is always represented in more than one nerve root, usually two, and to an unequal extent in these.

12. When the same muscle is represented in two nerve roots, the muscle fibres innervated by one root are not innervated by the other.

### 2. *Ablation Experiments.*

1. Division of any given nerve root produces paresis of the group of muscles supplied by it.
2. This paresis is only temporary, and soon passes off almost completely.
3. Such division of a nerve root does not result in incoordination of the remaining muscular combinations represented in other nerve roots.

### 3. *Exclusion of a certain Root or Roots during an Epileptic Spasm in the Limb (the Root being divided at the time, and not some time previously.)*

1. Division of one or more nerve roots produces alteration of the position of a limb during an epileptic spasm, which altered position depends on the particular muscular combinations that have been thus thrown out of action.
2. No incoordination is produced in the action of the remaining muscular combinations.
3. There is no evidence of overflow of the impulses which ought to travel down the divided root, into other channels through the spinal centres so as to reach the muscles by new paths.

### 4. *Degeneration Method.*

1. These experiments confirm the anatomical facts that had been previously ascertained by dissection, as to which nerve roots supply any given nerve with fibres.
2. The degeneration which results in the nerves is not a scattered one, but is localized to distinct bundles of nerve fibres occupying a certain position in the transverse section of the nerve.
3. The Wallerian law of degeneration, so far as it is applied to the nerve roots and their intervertebral ganglia, is found to be erroneous, for when a nerve root is divided on the distal side of the intervertebral ganglion not only is degeneration found in the peripheral end of such a root, but also in that portion of the sensory root between the ganglion and the spinal cord; pointing to the probability that there are certain nerve fibres which do not depend on the ganglion for their trophic supply, but

derive the same from elsewhere, either the spinal cord at another level, or the periphery.

In conclusion I wish to call special attention to the value of the method of excluding one or more nerve roots during an epileptic spasm, as affording us a means of confirming the facts that have been previously observed from stimulation of the nerve roots, and also of ascertaining new facts with regard to them and the plexuses which they form. It supplies us with a valuable means of studying the manner in which conduction of impulses from the cortex through the nerve roots and plexuses to the muscles takes place. Further, the method is capable of still wider extension; as if instead of producing general epilepsy, we apply less powerful stimuli to the centres for different movements, as represented in the motor cortex, we shall be able to connect such centres or parts of these with the nerve roots to which fibres proceed from these cortical motor centres.

## Description of Plate 10.

Fig. 1.—This figure is from a photograph of the brachial plexus of the Dog, and shows a portion of the cervico-dorsal cord, the nerve-roots which spring from one side of it, and the nerve trunks derived from these nerve roots.

*Sp. C.* = Spinal cord.
*V.C.*, *VI.C.*, *VII.C.*, *VIII.C.* } Represent the fifth, sixth, seventh, and eighth cervical nerve roots.
*I.D.*, *II.D.* } Represent the first and second dorsal nerve roots.
*Ph.* = Phrenic nerve.
*S.* and *I.Sc.Br.* = Supra- and infra-scapular nerves.
*C.* = Circumflex nerves.
*M.S.* = Musculo-spiral nerve.
*M.C.* = Musculo-cutaneous nerve.
*M.* = Median nerve.
*U.* = Ulnar nerve.
*Pect.Br.* = Pectoral branches.

Fig. 2.—This figure is from a photograph of the instrument which was devised to control the movements at the shoulder and elbow joints when those at the wrist and digital joints were being studied. The instrument proper is to the right in the figure, while that to the left is the ordinary instrument which is used to fix the animal's head in most experiments.

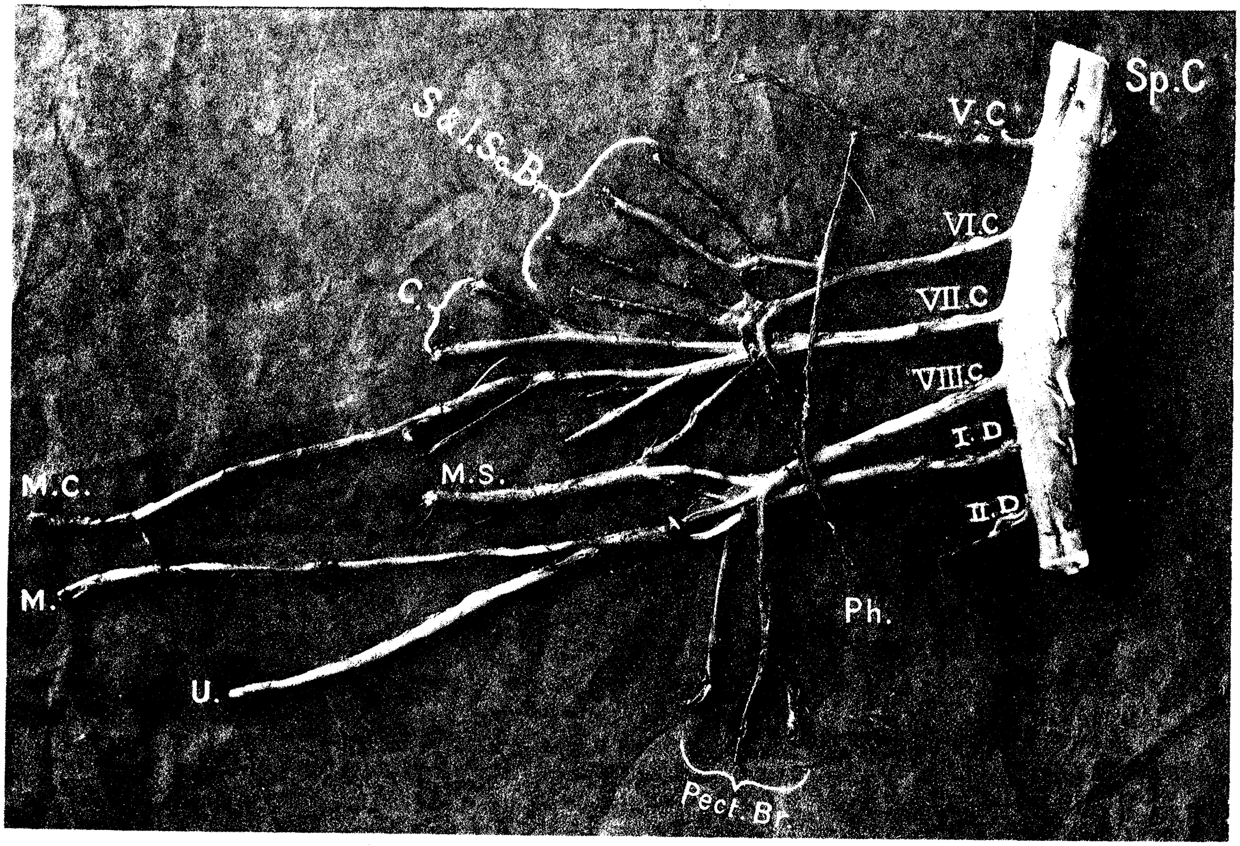



Fig. 1.

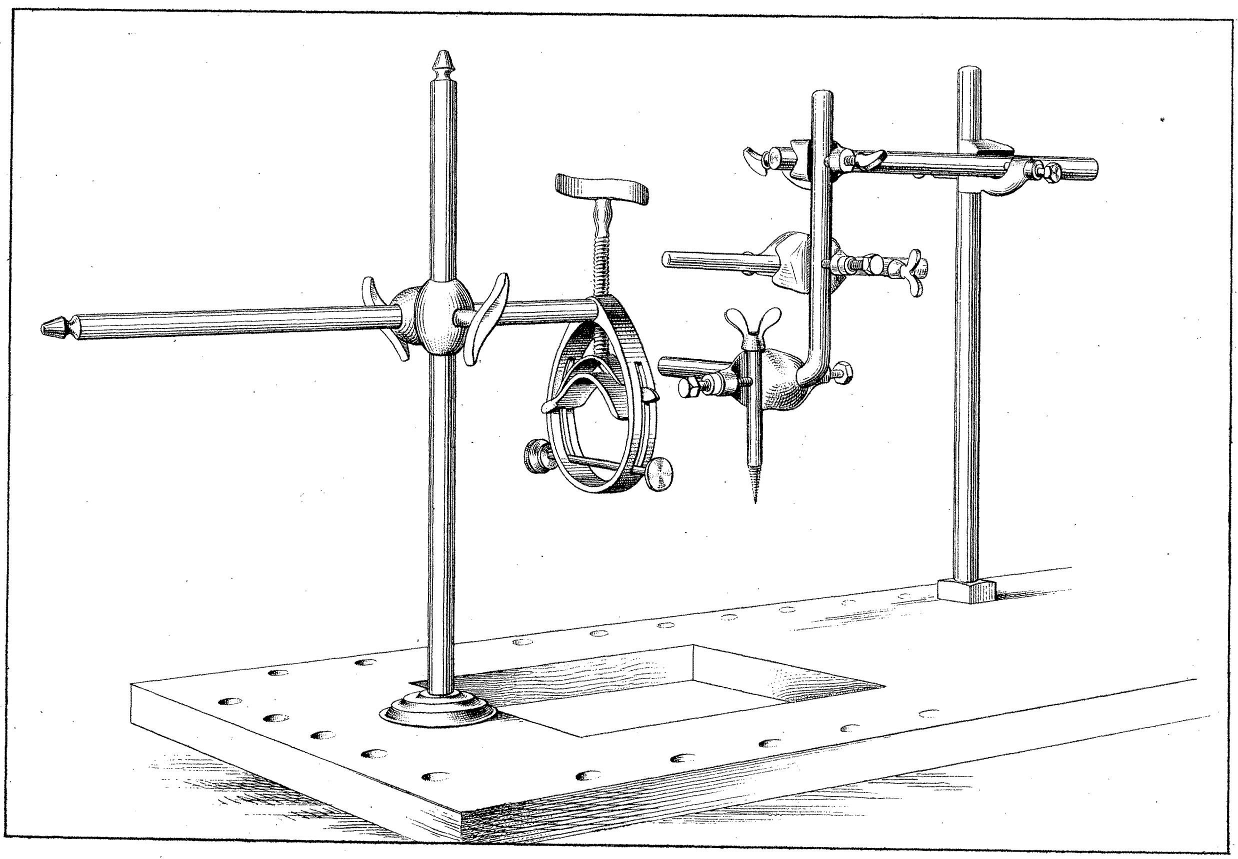
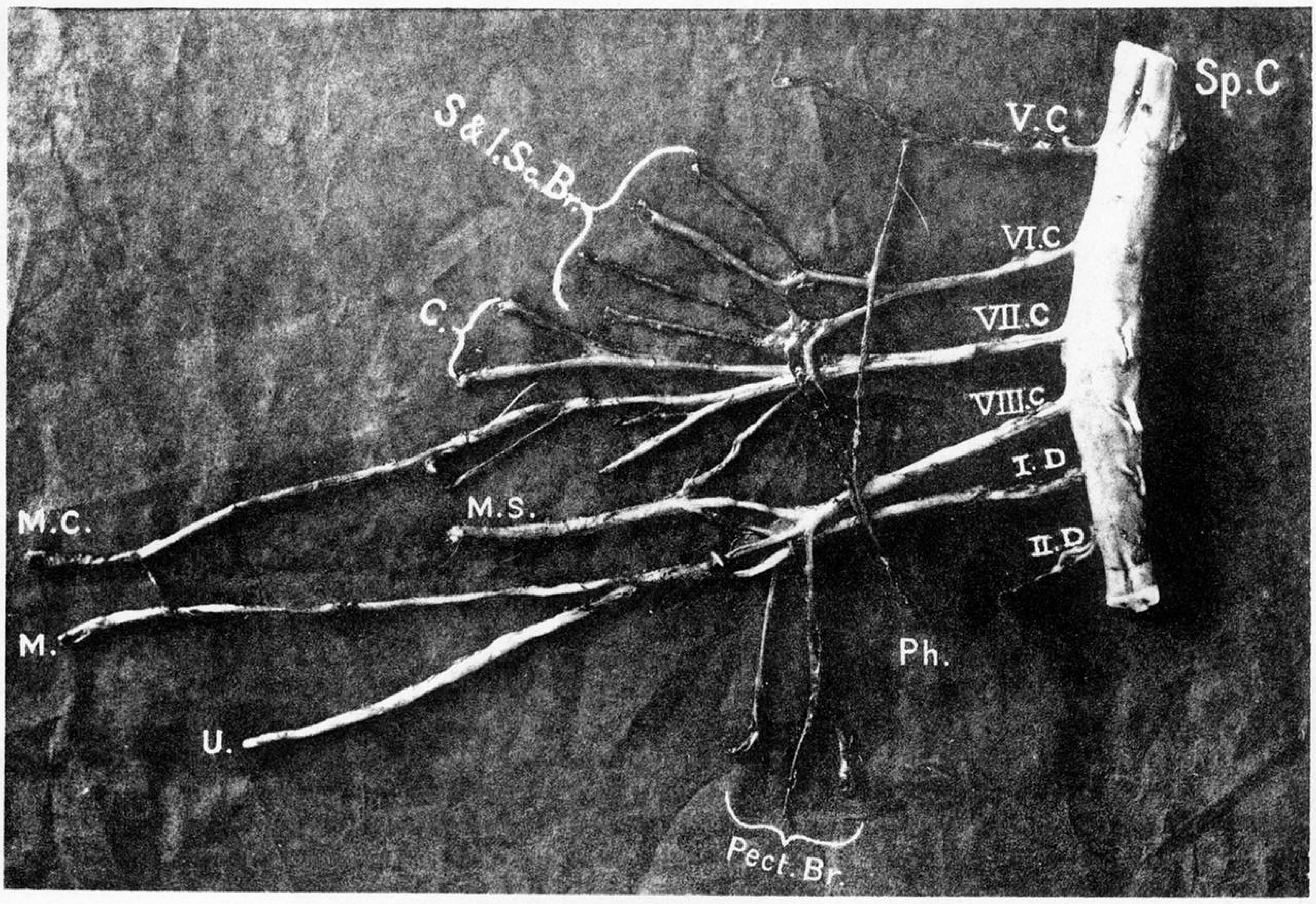


Fig. 2.



Cambridge Engraving Company.

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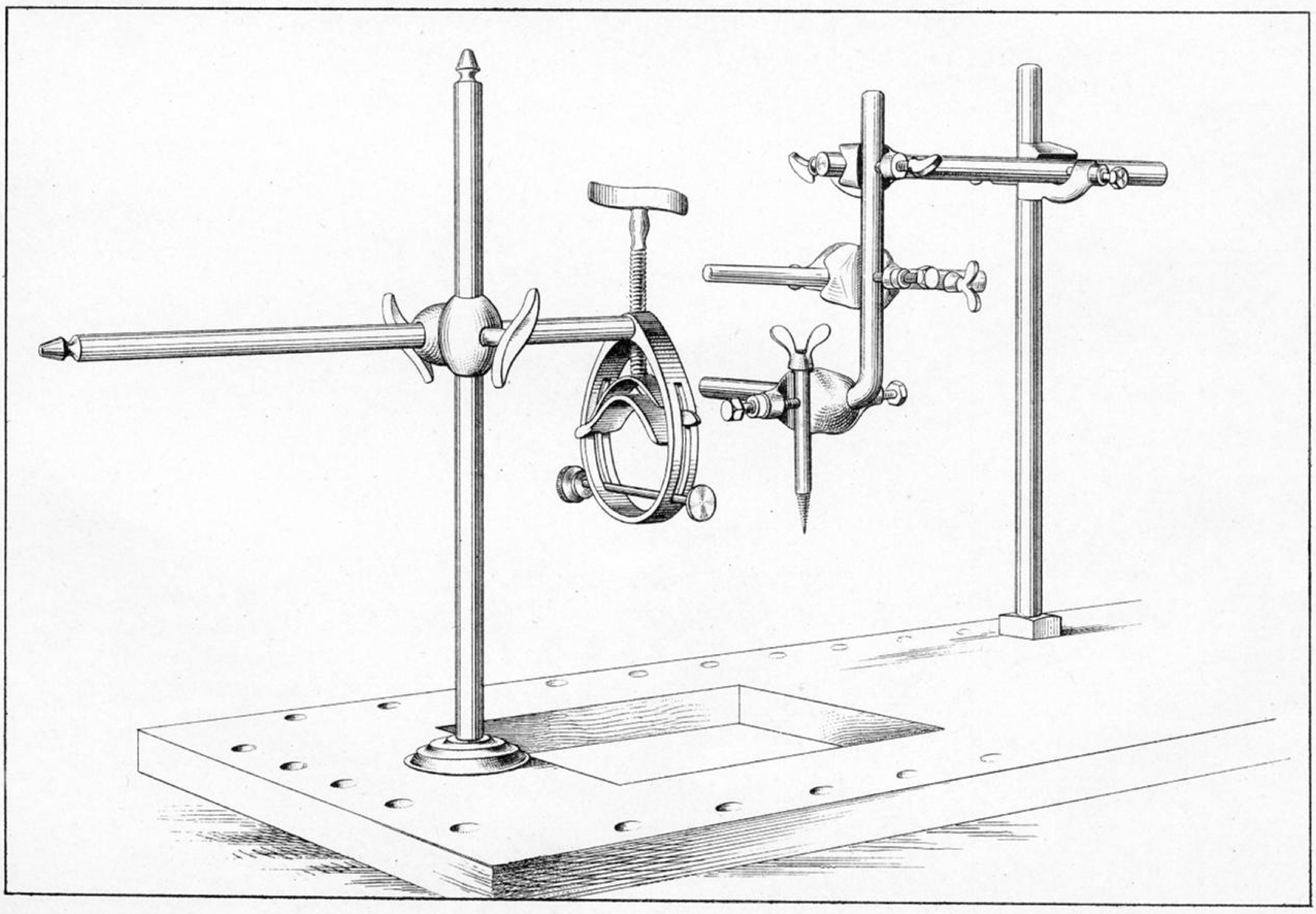

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