II. *Experiments in Examination of the Peripheral Distribution of the Fibres of the Posterior Roots of some Spinal Nerves.*—Part II.

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2.9.98.

INTRODUCTION.

The present research has been directed towards further examination of the distribution of the spinal nerve-roots. It has been pursued in continuance of previous* experiments dealing with the spinal pairs below the brachial. The communication treats of especially the skin-fields of the cranial and cervico-brachial nerves. In order to obtain a more perfect idea of the scheme of distribution of each entire spinal nerve

* Sherrington, 'Phil. Trans.,' B, vol. 184, p. 641, 1892.

the muscular fields of the spinal nerves of the limb region have been concurrently determined by separate experiments. Finally, these motor and sensory fields having been delimited, and thus the requisite prelimen to the original aim of the inquiry carried through, the examination of certain spinal reflexes has been proceeded to. I beg to sincerely thank Professor MICHAEL FOSTER for his kind encouragement throughout.

SECTION I.—DISTRIBUTION OF CRANIAL AND CERVICO-BRACHIAL NERVES TO SKIN AND TO MUSCLE.

PREVIOUS OBSERVATIONS.

On the sensory distributions of the cervical and brachial nerves of the Monkey there exist no previous observations. On that of the cranial Vth, ALDREN TURNER and FERRIER* have not long since published experiments; not, however, undertaken for the same purpose, nor dealing with the same portion of the subject as my own. On the motor distribution of the brachial nerves there only exist the original observations by FERRIER and YEO,† and the later and less detailed by FORGUE and LANNEGRACE.‡ These I have abstracted in a recent paper,§ and will not therefore recapitulate here. A certain number of observations on the distribution of the lowest brachial nerves were included in my own previous papers,|| and a part of the present results have been referred to in a paper by my friend, Dr. HENRY HEAD,¶ to whom though they were not perfectly complete at the time, they presented interest for comparison with his own clinical observations. The anatomy of the brachial limb is sufficiently alike in Monkey and Man to invite collation of results yielded by experiment on the former with the dissections of HERRINGHAM,** and with the clinical investigations of THORBURN,†† HEAD,‡‡ MACKENZIE,§§ STARR,|||| BRUNS,¶¶ and others carried out upon the latter.

* 'Phil. Trans.,' B, vol. 185, p. 719.
† 'Proc. Roy. Soc.,' London, 1881.
‡ 'Compt. Rend. Acad. d. Sc.,' Paris, 1884.
§ 'Journ. Physiol.,' Cambridge, vol. 13, 630, 1892.
|| 'Journ. Physiol.,' *loc. cit.*, 'Phil. Trans.,' *loc. cit.*
¶ 'Brain,' London, 1894, 339, 480, pt. lxvii., *cf.* figs. 59 and 60, chap. v., p. 474.
** 'Proc. Roy. Soc.,' London, 1887, p. 440.
†† 'Brain,' London, 1890.
‡‡ 'Brain,' London, parts lxi., lxii., 1893; lxvii., 1894; lxxiv., 1896.
§§ 'Journ. Path. and Bacteriol.,' 1893.
|||| 'Brain,' London, 1894, pt. lxvii.
¶¶ 'Arch. f. Psychiat.,' Berlin, vol. 24, p. 1.

METHODS OF EXPERIMENTATION EMPLOYED IN THE PRESENT RESEARCH.

Methods Employed.

The method of experimentation employed in the present series of experiments has been similar to that made use of in Experimental Series No. II. of my previous communication, and has been already described in that on pp. 46–49.* It has been designated by HEAD† the "method of remaining æsthesia," a convenient title which I gladly adopt. A certain number of experiments on the brachial plexus were given in Experimental Series I. B, of my previous paper, and in them the nerve-roots were severed just outside the vertebral canal. In the experiments of the present paper the nerve-roots severed were in every case exposed, and cut through inside the vertebral canal; in some instances the dura mater was not opened, and the whole spinal nerve—both its dorsal and ventral roots—was severed proximal to the spinal ganglion; more frequently the dura was laid open and then the particular dorsal (posterior) roots which it was desired to divide, were severed without interference with the ventral (motor) roots. In the majority of the experiments the animal was allowed to recover from the operation, and time was given for the wound to heal completely before the animal was finally examined and killed. Strict asepsis and profound anæsthesia were maintained in every experiment throughout the entire operative procedure.

With regard to the sections of the Vth cranial nerve a few words of description may be given. I have employed a method different from that elaborated by MAGENDIE‡ and BERNARD§ in the rabbit. "Cette opération est difficile par la raison simple qu'on ne voit pas ce qu'on fait." I use the same method as I employed for intercranial section of the oculomotorius,|| a method which offers the advantages that the nerve is seen at the time of section, can be divided deliberately either distal or proximal to the Gasserian ganglion, is exposed without removal or necessary injury to any part of the brain, or to any other cranial nerve, and leaves a wound which is comparatively trifling and soon healed. After a skin incision along the temporal ridge the temporalis is reflected in part, an ample trephine opening made in the temporal bone, and by lifting on wool pledgets the temporo-sphenoidal lobe the floor of the middle fossa of the skull is brought to view. Through the dura mater lining this the Gasserian ganglion and its three nerve-trunks are easily seen—more easily in *Mac. rhesus* than in *Mac. sinicus.* The only difficult branch to sever is the

* 'Phil. Trans.,' B., 1892, vol. 184.

† 'Brain,' London, 1894, p. 469.

‡ 'Journ. d. Physiol.,' vol. 1, 302, 1824.

§ 'Leçons s. l. Système nerveux,' vol. 2, pp. 48–57, 1858.

|| 'Proc. Roy. Soc.,' April, 1893.

ophthalmic, which it is not always easy to divide without doing damage to the other divisions. It is particularly easy to sever the whole nerve proximal to the ganglion.

For examining the distribution of the motor roots of the spinal nerves, one mode of procedure adopted was similar to one previously used in my examination of the lumbo-sacral plexus.*

The vertebral canal was opened, and a short series of the spinal nerves immediately above and immediately below the one to be investigated were divided; a sufficient time, usually 28 days, sometimes longer, was allowed for degeneration to have play; and finally, electrical excitation of the various nerve-branches in the limb itself was carried out. Strict asepsis and profound anæsthesia were maintained throughout the operative procedure.

In a certain number of experiments on motor distribution, the Wallerian degeneration was employed: the segmental nerve, the distribution of whose motor fibres it was desired to investigate, was cut completely through just after its exit from the spinal dura as far proximal to its spinal ganglion as possible. A sufficient number of weeks was then allowed for the progress of the degeneration: this time varied from 18 days to 30 days. The animal was then killed and dissected. The nerve twigs to the muscles were fixed and stained with osmic acid and then allowed to dissociate in methyl alcohol 40 per cent. in water. They were then exhaustively examined in teased preparations. Each nerve twig was completely examined, *i.e.*, the whole thickness of it teased up, mounted and preserved in a series of preparations. The accuracy, delicacy, and ease of this method surprised me not a little. It is greatly superior to the most perfect serial preparations of cross or longitudinal sections.

General Remarks.

The IIIrd, IVth, and VIth cranial nerves are distributed to muscles, and to these muscles probably distribute afferent nerve-fibres.† In regard to cutaneous sensation, these cranial nerves, as also the VIIth, VIIIth, IXth, XIth, XIIth, together with the sub-occipital nerve, now often called Ist cervical, can be left out of consideration: they possess no sensory skin-fields whatever.

All the other nerve-pairs possess each a sensory skin-field. In the description of the cutaneous fields, the terms employed in my previous communication‡ will be advantageous: of these a few special ones may be here defined :—

Mid-dorsal line of the body. Mid-ventral ,, ,, ,,	Lines along which the median vertical longitudinal plane of the body attains the dorsal and ventral surfaces of the body.

* 'Journ. Physiol.,' Cambridge, vol. 13, 658, 1892.

† Sherrington, 'Journ. Physiol.,' Cambridge, 1894 (also 'Proc. Roy. Soc.,' February 26, 1897).

‡ 'Phil. Trans.,' B, 1892, *loc. cit.*

Mid-dorsal line of the limb. Mid-ventral „ „ „	Lines on the dorsal and ventral surfaces of the limb, along which the skin-fields of the spinal nerves range themselves and behave as if at mid-dorsal (or mid-ventral) line of the body. These lines may be considered sideward extensions of the mid-dorsal and mid-ventral lines of the body into corresponding surfaces of the limb.

Throughout this paper, anterior means toward the head, posterior away from the head; the spinal nerve-roots, therefore, which are in anthropotomy frequently styled anterior and posterior, are here spoken of as ventral and dorsal.

The difficulty of obtaining suitable skin-points to serve as accurate and easily comparable indices of the absolute position of the sensory fields was mentioned in my previous paper.* In the head region, points of great value in this respect are furnished by the mouth and the pinna.

In describing the distribution of the nerves under the heading of each nerve pair possessing a cutaneous field, I give first the result of some one experiment thought typical for the nerve-pair. Then are appended any discrepancies between the results in the short series of individual experiments. To assist survey of the whole field of distribution of each entire spinal nerve—a survey of much importance for the understanding of the physiological anatomy of the animal—I have added to the description of the sensorial skin-field a concise account of the motor muscular field, determined in special experiments of my own. In the brachial and cervical region the muscular innervation in terms of spinal nerves is in the Monkey known only through the brief report by FERRIER and YEO,† and the later and less perfect results by FORGUE and LANNEGRACE.‡

FIELD OF THE FIFTH CRANIAL NERVE (*N. trigeminus*). Figs. 18, 20, 21, Plate 5; also fig. 2, p. 60; and figs. 4 and 5, pp. 66, 67, and sketch furnished to Dr. HEAD's paper, 'Brain,' *loc. cit.*, 1894.

Anterior Border.

The anterior border is coterminous with the anterior pole of the body.

Posterior Border.

The posterior border has been delimited in six individuals.

* 'Phil. Trans.,' *loc. cit.*, 1892.

† 'Proc. Roy. Soc.,' London, *loc. cit.*, 1881.

‡ 'Compt. Rendus, Acad. d. Sc.,' Paris, 1884.

Experiment. Macacus rhesus. ♀, young.

Measurements :—

Infra-pubic notch to umbilicus	=	11 centims.
Supra-pubic notch to umbilicus	=	8 centims.
Supra-sternal notch to umbilicus	=	12 centims.
Infra-sternal notch to umbilicus	=	7 centims.

The Ist, IInd, and IIIrd cervical nerves severed in the vertebral canal outside the dura mater.

The posterior edge of the upper field of response was several times delimited and yielded the following boundary.

"The boundary starts from the mid-dorsal line on the scalp at about the junction of the posterior with the middle third of the distance from the glabella to the external occipital protuberance. Thence it takes an almost rectilinear course to the base of the pinna about 4 millims. behind the anterior surface of that structure; the boundary then ascends the hinder (mesial) surface of the pinna, finally attaining to and winding over its upper edge. On the anterior (lateral) surface of the pinna,* the boundary descends a little in front of the fossa of the helix, sweeps forward below the concha to the tragus, and then dips over it slightly into the concha and winds out again in the notch between tragus and anti-tragus. (The auricle of Rhesus possesses scarcely any lobule.) Having thus left the ear, the boundary line proceeds along the outer face of the vertical ramus of the lower jaw, running slightly in front of the posterior edge of it. It crosses just in front of the angle of the jaw, and turns horizontally inwards toward the mid-ventral line of the neck, which it reaches a few millims. above the thyroid cartilage."

Sensory Disturbances produced by Section of the Vth Cranial, as observed in the Monkey.

Skin.

The whole of the side of the face in front of the anterior border of the sensory skin-field of the IInd cervical nerve (*vide infra*, under IInd cervical nerve, p. 68 and fig. 6, p. 69), is completely insensitive. Along the median line, the cross lap of the skin-field of the Vth cranial of the opposite side is everywhere slight, it is greatest on the scalp, amounting to, perhaps, 5 millims.; on the lip it is barely demonstrable.

When the animal drinks, which it does without apparent hesitation or difficulty, it begins by placing its muzzle fairly in the centre of the basin, but it then almost

* See Remarks, p. 57.

directly proceeds, while drinking, to shift its head sidewise in a direction away from the side of the nerve-section. This deviation of the head is only limited by the muzzle finally meeting the edge of the dish in the direction of the uninjured side, and against that it is kept, the draught continuing to be taken from the corner of the dish on that side. If the dish be shifted, when the animal starts drinking from it again he starts from the middle of the dish as before, and then gradually shifts over as before and to the same corner. The phenomenon seems attributable to the recognition of the food by sensory impressions arising from the muzzle, and from one side of it only, the eyes being too near to the pan to be used while the draught is being taken. The animal keeps turning its neck in the direction of the one side upon which the food is actually felt, believing the food to lie chiefly in that direction. Space-perception here, therefore, depends much on trigeminus.

The Tongue.

Sensation is completely abolished on the dorsum of the tongue, from the tip backwards, to just in front of the circumvallate papillæ. When the trigeminus of one side only is severed the area whence no response to touching, or pinching, or heat can be elicited, has the limits represented in fig. 1. It will be noticed that th posterior border is a sloping one, running parallel with, and about 2 millims. in front of the row of circumvallate papillæ. It will be also noticed that the field extends apparently fully up to the median line, in other words an overlap of the fields of the right and left trigeminal nerves (crossed overlap) across the median line of the dorsum of the tongue is very slight or non-existent.

The frenum and the side of the tongue, except behind the level of the line of circumvallate papillæ, give no response to mechanical or thermal excitation.

The Gums and Inside of the Cheek.

The gums on the side of the section give no response to mechanical or thermal excitation, neither does the mucous membrane lining the cheek, which is in the Monkey peculiarly sensitive.

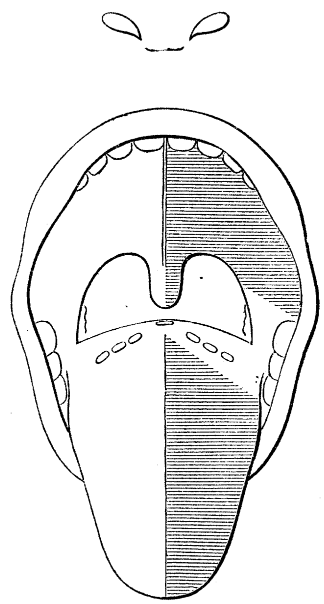
The Palate.

The half of the hard palate corresponding with the side of the nerve-section gives no response to mechanical or thermal excitation. So also the half of the soft palate and of the uvula. On the other hand the surface of the anterior pillar of the fauces and of the tonsil are fully sensitive. On the palate, as on the tongue, the anæsthesia extends up to the median line, so that a crossed overlap of right and left fields must in this region be very slight or may not exist.

Taste.

After section of the Vth cranial I have always failed to obtain evidence from the Monkey of persistence of any sense of taste. Monkeys normally react briskly to quinine or cayenne placed upon the tongue. After the intracranial section of the trigeminus the sensitiveness of the front two-thirds of the organ seems lost to these substances as well as to mechanical and thermal stimuli. Either the chorda tympani contains no gustatory fibres, or the gustatory fibres existing in it are in some way derived from the trigeminus; this latter supposition appears on anatomical and

Fig. 1.



morphological grounds hardly possible. It is hardly possible to obtain from experiment upon laboratory animals any minute evidence about the sense of taste, but my experiments point clearly to abolition—complete removal—of the sense of taste in the anterior two-thirds of the tongue, *i.e.*, in front of a line a few millims. anterior to the circumvallate papillæ. After intracranial section of the Vth the sense of taste *behind* that line still remains intact. This indicates that the gustatory fibres in the glosso-pharyngeal are not traceable to the trigeminal root, and that the gustatory and tactile fields of the two nerves are, on the dorsum linguæ, coterminous.

The Nose.

The crossed overlap along the bridge of the nose is distinct though slight. The nasal mucous membrane, as far inward as can be examined easily from the nostril, gives no response either to mechanical or thermal excitation after intracranial section of the trigeminus.

The Eyes.

I have been struck by the fact that, contrary to the statement by MAGENDIE, no noticeable disturbance or ataxia results in the motions of the eyeballs in consequence of section of the trigeminus, even after bilateral section.

Remarks.

The agreement between the results obtained for this nerve in the separate experiments has been close as compared with those obtained for some other nerves. The most striking exception has been in regard to the extension backward of the field in a young male Rhesus. In this individual the posterior boundary lay further back than in all the other experiments; it included evidently a larger area than usual, into which the whole of the fossa of the helix of the pinna, and in the neck it reached the mid-ventral line on the thyroid cartilage instead of at a point altogether above that cartilage.

It must be remembered that in the above experiments, which illustrate by the method of the remaining æsthesia the skin-field of the Vth nerve, the roots of the vagus as well as of the Vth were left untouched. After intracranial section of the vagus roots in addition to the severe operation necessary for section of the cervical nerves, the condition of the animal precludes satisfactory examination of the cutaneous fields, so that exploration under those circumstances proves fruitless. There is, therefore, from the field above described as that of the Vth cranial, possibly to be deducted a small portion of the pinna in the immediate neighbourhood of the external auditory meatus. Whether the small field immediately surrounding the external meatus belongs to the vagus nerves and anywhere extends beyond the actual limits of the field of the Vth cranial is doubtful, but it may do so, and if it does the boundary given in my above experiments to the field of the Vth cranial extends on the middle of the outer face of the pinna somewhat too far backward, and is really there a combined boundary due to Vth and vagus together. The accompanying figure (fig. 2) shows the limits of the vagus field on the pinna, and also that of the field left when the Vth cranial as well as the vagus remains intact. The sketch is combined from experiments made on eight individuals, but in none of the individuals was the combined field first taken and then the isolated field due to vagus only, because the shock accompanying such a procedure precludes satisfactory exploration of the surface.

Of the whole Vth nerve only the *ramus mandibularis,* includes in its sensory field the pinna, and it includes, as above mentioned, only a portion of the pinna. The boundary of the skin-field of the Vth at first sight seems, where it crosses the pinna curiously irregular and arbitrarily placed. I find its course is, however, such as to include all those parts which are traceable to the tissue of the mandibular arch and none of those traceable to the hyoidean. This can be well-appreciated by tracing the boundary of the skin-field of the Vth on the figures of the development of the human pinna by W. HIS, jun.* On the pinna, therefore, the field of the Vth cranial nerve extends to, but does not trespass across the first visceral cleft, and the skin-field of the 3rd division of the nerve (*ramus mandibularis*) in so far accurately justifies the name mandibular.

The field of cutaneous distribution of the *trigeminus* possesses particular interest from GASKELL'S suggestion that the huge sensory root of the nerve is compounded of a series of originally separate cranial sensory nerves secondarily massed together. The large area of the cutaneous field would then be really compounded of several segmental fields; each of these it might be possible to separately determine by appropriate section of the other divisions of the nerve. The intra-medullary course of the nerve-fibres arising from the Gasserian ganglion has for some of them been traced down to the level of the IInd cervical segment of the spinal cord. As regards juxtaposition and overlap, it will be shown that the skin-fields of the Vth cranial and of IInd cervical mutually behave as if the two nerves were immediately juxtaposed members in a spinal series, without intercalation of any intermediate segment.† All that part of the skin-field of the Vth cranial which is overlapped by the field of the IInd cervical is, of course, segmentally posterior to the rest of the field. Of the large area not so overlapped it was interesting to inquire from the sensory cutaneous supply which part might be segmentally anterior, which posterior. The sensory fibres for even the conjunctiva and cornea are traceable to quite low, in the floor of the fourth ventricle, and even to the top of the spinal cord itself. I have seen anæsthesia of the conjunctiva and cornea ensue upon section of the so-called ascending, really descending, root of the Vth at the level of the *calamus scriptorius*.‡ It is worth inquiring whether the three great divisions of the trigeminus springing from the Gasserian ganglion may not themselves be segmentally collected portions of the nerve, each representing one or more complete cranial sensory roots. If so, the three great peripheral divisions will each possess a zonal skin-field extending from mid-dorsal line to mid-ventral line. To examine this point, the delimitation of the skin-field belonging to each of the three divisions of the Vth was undertaken.

* W. HIS, jun. "Zur Entwickelungsgeschichte des Acustico-facialis Gebietes beim Menschen." 'Archiv. f. Anat. u. Physiol.,' Anat. Abth., 1889. Supplement-Band.

† In this statement the tiny and segmentally incomplete field of the vagus, described p. 64 is intentionally left out of account.

‡ SHERRINGTON, 'Journal of Physiol.,' vol. 14, pp. 293, &c., 1892.

FIRST DIVISION OF THE VTH (*Ramus ophthalmicus*). See fig. 18, 21, Plate 5, and fig. 2 in text, and sketch furnished to Dr. HEAD'S paper, 'Brain,' *loc. cit.*, 1894.

The skin-field belonging to this division of the Vth cranial nerve has been separately isolated in two individuals; the results of the two experiments agree very closely indeed.

Experiment.—M. rhesus. Male, young. 15.9.1893.

Measurements :—

Supra-sternal notch to pubic crest	25 centims.
Acromion process to tip of middle digit	31 „

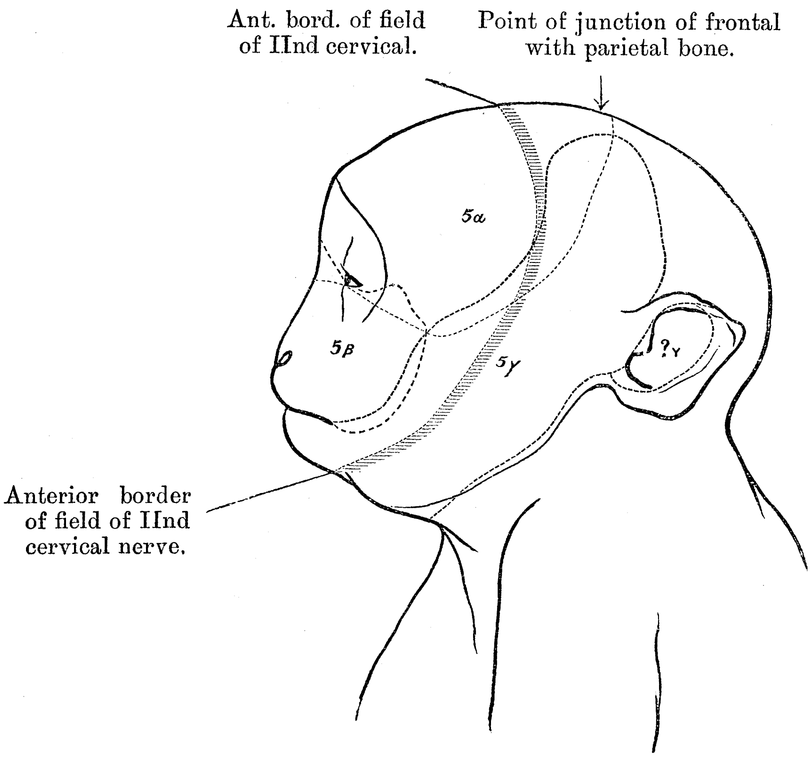
At 9.20 A.M., the posterior roots of the IInd, IIIrd, and IVth cervical nerves of the right side, and the inferior and middle divisions of the right Vth cranial nerve, severed after the dura mater had been opened. At 5.30, the isolated field supplied by the *ramus ophthalmicus* finally delimited.

"The isolated field of response lies above and lateral to the palpebral fissure. It is bounded by a line which, starting from the mid-dorsal line of the head at a level about 1 centim. behind the bregma and just in front of a transverse line joining the highest points of the roots of the right and left pinnæ, sweeps laterally in a rectilinear manner. Having reached a point about ·5 centim. above the level of a line drawn from the outer canthus of the palpebral fissure to the external auditory meatus, and in a vertical about 13 millims. in front of the front edge of the root of the pinna, the boundary of the field slopes downward and forward to a point at which the following two lines cross: α, line from angle of mouth to top of root of pinna; β, line from outer canthus to the angle of the lower jaw. From this point it runs horizontally forward for a centimetre or more, and finally it ascends, sloping forward, to the free edge of the lower lid, attaining it a little to the lateral side of the middle point. Winding over the free edge of the lid, it continues to slope inwards on the conjunctival surface, and finally emerges at the inner canthus, without the border having invaded at all the ocular conjunctiva; that is, the whole ocular conjunctiva is included in the field of the first division of the Vth. On the bridge of the nose the boundary slopes downward and inward, so that it reaches the crossed overlap from the field of the nerve of the opposite side. It was not found that the tip or any part of the lower 3 centims. of the nose was supplied by the ophthalmic division of the trigeminus. About 1·5 centim. above the opening of the nostril, the internal surface of the nose, both on the septal and on the lateral walls, responded to touch; these must, therefore, be supplied by the *ramus ophthalmicus*. The hard palate and the greater part of the soft palate gave no response; the extreme posterior edge of the soft palate certainly responded to touch; this response persisted after final section of the whole trigeminus. There was distinct photophobia of the right eye, but no vascular injection and no abnormal degree of lacrymation. There was no obvious difference in size between right and left pupils."

Another experiment yielded almost absolutely identical results.

To ascertain the field of the 2nd division (*ramus maxillaris*), the IInd cervical nerve was divided, and the 1st and 3rd divisions of the Vth. The area of response upon the face obtained in this way was bounded by a line which commenced at the crossed overlap on the middle line at the top of the root of the nose, *i.e.*, on the frontal bone about the level of the superior edge of the orbits, or about the region of the human glabella. From this point the boundary sloped rapidly down to the inner canthus of the eye, crossing the most median portion of the upper lid to attain the canthus: it

Fig. 2.



?v indicates the field attached to the vagus nerve.

...... the limit of the 1st division of the Vth, 5α.
------ the limit of the 2nd division of the Vth, 5β.
-.-.-. the limit of the 3rd division of the Vth, 5γ.

then ran along the conjunctiva of the inner face of the lower lid, and at the outer canthus crossed upward over the upper lid, so as to include in the field the most lateral sixth of that lid. It then turned horizontally outward over the malar prominence, and, after extending along a good third of the line from the outermost point of the orbital opening to the external auditory meatus, bent downward and then swept toward the angle of the mouth; this it reached from below, so as to include the extreme lateral edge of the lower lip; it runs almost horizontally along the inner surface of the cheek to the maxillary gums. Along the middle line, both at lip and nose, the crossed overlap is very small indeed.

To delimit the 3rd division (*ramus mandibularis*), the following experiments were made:—The IInd and IIIrd cervical roots were cut in the vertebral canal, and the 1st and 2nd divisions of the Vth just distal to the Gasserian ganglion. The anterior boundary of the field of response then ran from the angle of the mouth to the anterior end of the lower border of the zygomatic arch; between these points the lower part of the curve is slightly concave forward, the upper part slightly convex forward. Ascending then upon the temporal muscle, the course taken is again that of a line with a slight concavity forwards. The vertex is approached most nearly opposite the junction of the coronal and sagittal sutures (bregma); the middle line is, however, not actually reached. I have paid particular attention to this point in three experiments, and am convinced that the field of the mandibular division of the Vth, although it approaches near to the middle line of the scalp, does not actually attain to it. It however extends higher than as given for Man in FLOWER'S atlas of nerve fields. The boundary becomes identical with the posterior boundary of the skin-field of the entire Vth about 3 centims. from the mid-dorsal line; after that junction the boundary is that described above under the posterior boundary of the skin-field of the Vth on page 54. The control experiment of estimating the field of the 3rd division, and then severing the nerve, I have carried out once. On severing the 3rd division, the anterior boundary of the field which had previously lain between the angle of the mouth and the zygoma retreated to the pinna of the ear, ramus of jaw, and thyroid cartilage (*vide infra*, p. 71, IIIrd cervical nerve).

From these experiments it becomes obvious that if to the three divisions of the Vth cranial we apply as a test for complete segmental character the fact found to hold good for all complete spinal sensory-nerves, *i.e.*, that the skin-field of a complete segmental nerve extends continuously from the mid-dorsal line of the animal to the mid-ventral line, the test gives, as regards the three divisions of the Vth cranial, a distinct reply. It is impossible to mark exactly the anterior polar point of the body, *i.e.*, that point in the anterior end of the animal which occupies a position there similar to that held by the tip of the tail in the posterior end of the animal; that being so, it is impossible to say whether the skin-field of the *ramus ophthalmicus* does really reach the mid-ventral line of the body; it certainly occupies some of the mid-dorsal line, but the anterior pole of the body being the place of junction of the mid-dorsal with the mid-ventral line of the body, to admit ignorance of the position of the anterior polar point is tantamount to admitting that we do not know where the mid-dorsal line ends and the mid-ventral line begins. Not being able to say, therefore, whether the field of the *ramus ophthalmicus* does extend to the mid-ventral line, we cannot apply the test confidently to it. In the same way we cannot say whether the *ramus maxillaris* of the Vth extends to the mid-dorsal line.

although we can be certain that it does extend to the mid-ventral line. The only conclusion that results from the application of the test to the skin-fields of these two nerves is, therefore, that if one of them is a complete segmental field, then the other cannot be, because there are not *two* anterior polar points to the body.

But if either of these two fields is a complete segmental one, and is at the same time overlapped by the field of the IInd cervical nerve, then the remaining one of the two fields cannot be overlapped by the field of the IInd cervical; at least, no such extent of overlapping is evidenced in other parts of the body. On the other hand, if the two fields be neither of them, when considered separately, complete segmental fields, but be both merely portions of one segmental field, each of them might be well overlapped by the complete segmental field behind, namely, that of the IInd cervical nerve.

Examination of the fields shows that each is overlapped by the field of the IInd cervical nerve, though that of the *ramus ophthalmicus* constantly and to a greater extent than that of the *ramus maxillaris*, rarely and minutely overlapped. This part of the test indicates, therefore, that the combined skin-fields of the 1st and 2nd divisions of the trigeminus may be together equivalent to the field of a complete posterior root of a segmental (spinal) nerve, but that neither of the fields is so when taken singly.

But the skin-field supplied by the 3rd division of the nerve is, like those supplied by the 1st and 2nd divisions, overlapped from behind by that of the IInd cervical nerve, and to a far greater amount than they. This argues for the skin-fields of the first and third divisions of the trigeminus belonging to the same segmental level, and for no one of them by itself constituting a complete segmental area. Further, to the skin-field of the *ramus mandibularis*, the test for a complete segmental skin-field, namely, that it extends from mid-dorsal line without a break to the mid-ventral line, can be applied with certainty, since its position in regard to those lines is not dubious. The field, as a fact, occupies the mid-ventral line along a considerable length; but it does not actually attain the mid-dorsal line anywhere, although it approaches on the scalp at one point somewhat closely (see p. 61). It is, therefore, very unlikely that this field is of complete segmental character.

A third feature in which the separate skin-fields of the three divisions of the trigeminus differ from the fields of complete segmental (spinal) nerves is the following: The overlapping of fields of contiguous spinal nerves is regular and very considerable; the contiguous skin-fields may have half of their respective areas in common. With the fields of the three divisions of the trigeminus the extent of mutual overlap is irregular and not nearly so great. Thus, on the conjunctiva the fields of the 1st and 2nd divisions meet, but *hardly overlap at all;* similarly those of the 2nd and 3rd divisions at the angle of the mouth. I do not know of detailed observations on the mutual overlap of the skin-fields of peripheral nerves, but in respect of their mutual overlap the skin-fields of the cranial Vth are very different from the skin-fields of complete segmental (spinal) nerves, and the skin-fields of peripheral nerve-trunks, as far as I have myself investigated them, resemble in this feature the divisions of the trigeminus (see below, p. 101).

Analysis of the sensory portion of the cranial Vth nerve, therefore, by this method fails to resolve it from a single segmental nerve into a series.

The fact that the fibres of the sensory root of the trigeminus, namely, the fibres running proximally from the Gasserian ganglion, have a long region of origin (from the mid-brain in front to the level of the IInd cervical nerve behind) also fails as an argument in proof that the nerve belongs to a number of metameres. The fibres from the root ganglion of a spinal nerve grow into the central nervous axis, and there penetrate to various distances, becoming connected with not one segment, but with many; thus, those of the sacral ganglia reach even to brachial and to bulbar segments. As regards the so-called surface origin of the sensory spinal root, it is not very uncommon to find filaments of the hinder of two nerve-roots crossing filaments from the root next in front, demonstrating to the naked eye the insufficiency of the surface origin of the root to serve as criterion of segmental position, *cf. infra*, p. 145.

It is the position of the ganglion, and not that of the so-called spinal "origin," that is the key to the segmental position. In other words, *the situation of the nerve-cells, not that of the nerve-fibres, marks the segmental position of the sensory nerve.* Growing out from the ganglion-cells, its fibres wander distally into skin and muscles, and these trespass, as I have pointed out, considerably beyond the limits of their proper metamere, for they considerably overlap. Centripetally they extend even more boldly into regions outside their original metamere, in fact, into segments quite remote. A similar arrangement exists in motor nerves, but I* and A. S. F. GRÜNBAUM† have pointed out that the region of spinal origin of the fibres of a motor root, unlike that of the sensory root, is of strictly local extent in the spinal cord, confined to one, its own, segment. That is to say, the seat of the motor cells of the segmental nerve is, like that of the sensory cells of the segmental nerve, not pluri-segmental, but confined to one, the original, segment. The nerve-cells of a metamere do not wander beyond the confines of the metamere in which they arise, but the nerve-fibres rising from them are eventually in great part thrust quite beyond the confines of the original metamere. This trans-segmental trespass of the nerve-fibres is comparatively slight in the skeletal musculature of the trunk, distinctly greater in that of the limbs, especially at the free apex of each limb, greater still in the sensory structures of the skin, and yet greater in the distribution of efferent fibres to the vertebral ganglia of the sympathetic, but greatest in the sensory fibres distributed from the root ganglion to the segments of the spinal cord.

In a previous paper I have insisted on the want of segmental correspondence between the distribution of the sympathetic efferents of the motor spinal root and

* 'Journal of Physiology,' vol. 13.

† 'Journal of Physiology,' vol. 15.

the cutaneous distribution of the fibres from the cells of the corresponding spinal ganglion. To LANGLEY we owe the suggestion (1891), and the demonstration (1893), that there is, on the other hand, close correspondence between the field of cutaneous distribution of the efferent fibres arising in a vertebral ganglion of the sympathetic and the cutaneous field of distribution of the fibres of the corresponding spinal ganglion. I appended to my previous paper mention of observations undertaken by myself in pursuance of his discovery of this relationship. I cannot too distinctly disclaim the slightest pretension to having myself previous to him put forward the view of the correspondence existing between the skin-field of the sympathetic ganglion and that of the spinal ganglion. I am induced to state this emphatically, because in an abstract of my paper by a foreign reviewer the doctrine is accredited to myself, and not to its real author, Dr. LANGLEY.

VAGUS (?) NERVE. (Fig. 3.)

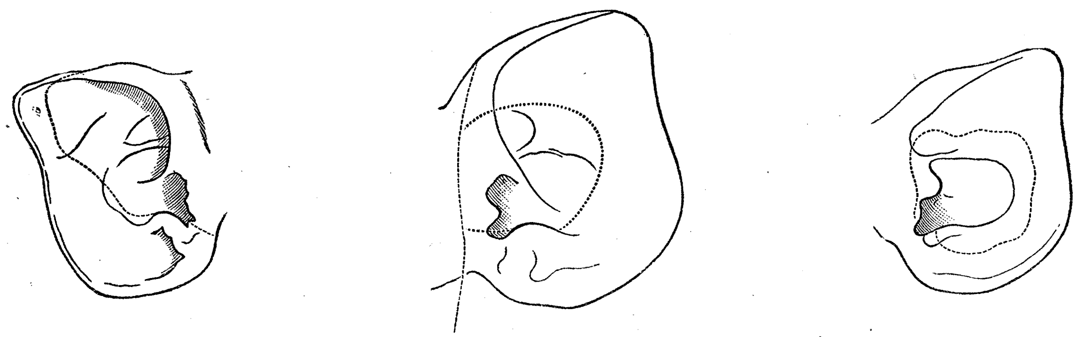
After the Vth cranial and the highest three cervical nerves have been completely severed, the skin of the external auditory meatus, and just round it, still remains sensitive. I think there is little doubt that this must be due to the still unsevered vagus nerve with the auricular branch from its "ganglion of the root." I have not, however, succeeded in obtaining an animal in sufficiently good condition after the operation of intra-cranial section of the vagus, in addition to intra-cranial section of trigeminus and section of the three highest cervical nerves to ascertain with certainty the disappearance of the field after section of all those nerves.

The field has been completely delimited in two experiments only; the operation required for revealing it is somewhat severe. Lying, as the small field does, wedged in between the large fields of the Vth cranial and the IIIrd cervical, and, as it were, imbedded in the anterior part of the field of the IInd cervical, it is, in order to isolate it, necessary to sever the Vth cranial at its origin, and also the highest three cervical nerves inside the vertebral canal. When this has been successfully accomplished, a patch of æsthetic skin is easily demonstrable on the ear. It includes and immediately surrounds the external auditory meatus. Its shape and size, in the two experiments carried out upon it, were almost identical. It takes in practically the whole of the concha, the antitragus, part of the tragus and part of the antihelix; also part of the fossa of the antihelix. Its limits can be better realised from fig. 3 than from verbal description. The surface inside the external auditory meatus was sensitive in my experiments as far inwards as could be tested with an ordinary probe.

This tiny area, confined to the lateral region and widely distant from both the mid-dorsal and the mid-ventral lines, differs curiously in these respects from the skin-fields delimited for all other cranio-spinal nerves. The area lies on the opening of the 1st visceral cleft. It is overlapped by the fields of the Vth cranial and of the

IInd and IIIrd cervical nerves. The auricular branch of the vagus is, by some authorities, considered the *ramus lateralis* of the vagus of lower vertebrates; its skin-field points, however, rather to its being a branchial branch. Its fibres, traceable by dissection to the ganglion of the root of the vagus, may or may not actually arise in that ganglion. In my experiments, the roots of the vagus have not been cut, for the reasons stated above. This skin-field offers the instance, unique in my experience, of a root distribution over an area absolutely isolated from the median lines of the body. It is the only true exception to the zonal type of distribution. It indicates in

Fig. 3.



Combined posterior border of Vth cranial and auricular of vagus (?).

Dotted line marks boundary of auricular of vagus (?). Broken line marks ant. edge of IIIrd cervical.

Completely delimited area of auricular of vagus (?).

the strongest way a very great difference between the vagus and the ordinary spinal nerves. I cannot help regarding it as evidence that the vagus is a visceral nerve, and supplies the visceral depth of the 2nd visceral cleft, just as the diagram, p. 56 *supra*, of the tongue and fauces shows the glosso-pharyngeal nerve supplying the depth of the 1st visceral cleft. That the field of the vagus comes so far toward the mouth of the cleft as to reach external auditory meatus is not extraordinary, when it is remembered how widely the posterior root-nerves over-run the limits of the segmental borders of their metameres.

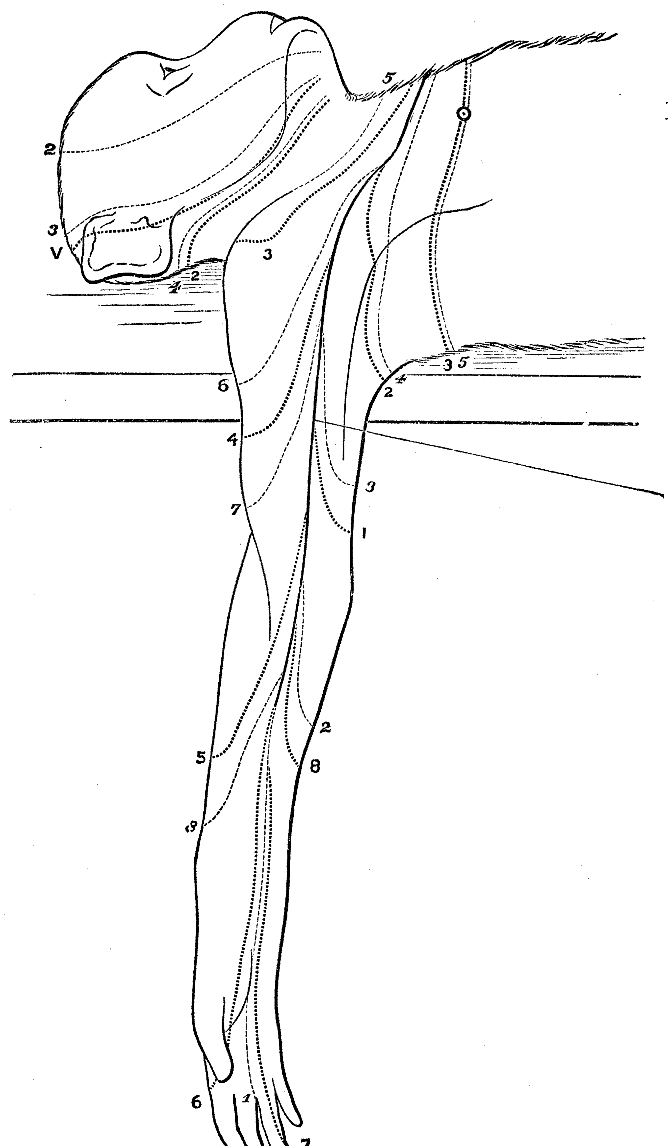
XIIth Cranial Nerve.

It was long since pointed out by Mayer, Luschka, Vulpian, and others that in various Mammals, including Man, the hypoglossal nerve occasionally possesses a dorsal root, and that this root possesses a ganglion. In the artiodactylous Ruminants and, to a less degree, in Carnivora this dorsal ganglionated root is regularly present,* although in the latter always small. Embryological study of the Mam-

* A. Froriep and W. Beck, 'Anat. Anzeig.,' vol. 10, p. 688, 1895.

malia reveals the fact that the XIIth cranial nerve throughout the class is originally a group of true spinal nerves, and that the dorsal roots of these, each provided with

Fig. 4.



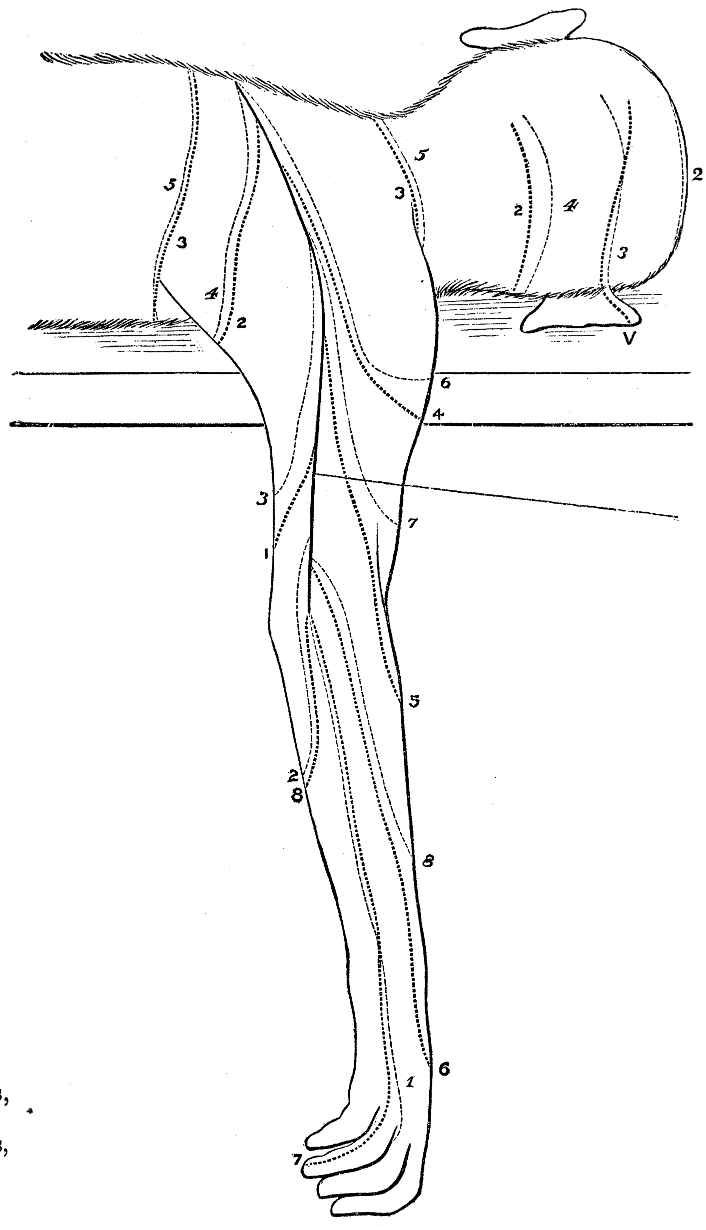
Nipple.

The mid-ventral line of the limb.

Anterior borders, light broken line.
Posterior borders, heavy dotted line.

a ganglion, atrophy; the ventral non-ganglionated roots, on the other hand, combine together to form the trunk of the hypoglossal nerve of the adult. The Macaque Monkeys (*rhesus* and *sinicus*) that I have examined have not shown any sign of this dorsal root. It is for that reason that, in discussing the source of the sensory fibres distributed to the external auditory meatus, I have not considered the fibres attributable to the XIIth cranial nerve. FRORIEP and BECK could not find it either in the Prosimiæ or in the Cynomorphous Apes.* In the Cat the Ist cervical has a small but distinct ganglion in the canal in the atlas.

Fig. 5.



The mid-dorsal line of the limb.

Anterior borders, light line.
Posterior borders, heavy line.

Ist Cervical Nerve.

No skin-field at all has been found for this nerve in either of two individuals especially examined for the field. On dissection I have never met with any nervous filaments belonging to it entering the cord in the line of the sensory roots of the

* *Loc. cit.*

other cervical nerves. The only nerve-filaments existing have been to all appearance those of ventral roots; they are not numerous; they are gathered to a single nerve-trunk, which passes through a small foramen in the transverse process of the atlas.

In *Macacus rhesus* and *sinicus*, therefore, the so-called Ist cervical nerve, the sub-occipital, possesses no dorsal (afferent) root, and, as a consequence, no sensory skin-field; my observations, however, have not been numerous enough to do more than determine what is the general rule; it is possible that occasionally the Ist cervical possesses a posterior root, whether that then has a skin-field must remain an open question; its distribution may be confined to muscles, ligaments, &c. As is well known, the Ist cervical nerve in Man does occasionally possess a small dorsal (afferent) root on which is the usual spinal ganglion. In the Chimpanzee this dorsal root and ganglion is usually present, but not in the Orang, nor in the Cynomorphic Apes.* In the Dog and Cat the ganglion and root are, as far as I have seen, always present; also in the Rabbit and Guinea-pig. In the Cat the field of this root includes the apex of the pinna.

Motor Distribution.

This has been examined in four individuals, partly by mechanical excitation of the motor root, partly by faradic excitation of the primary, ventral, and dorsal divisions near their origin as possible. The following are the results obtained: a certain amount of individual variation occurs, especially with regard to superior obliquus muscle.

Dorsal Primary Division.—Rectus posticus major, rectus posticus minor, obliquus inferior, obliquus superior, trapezius.

Ventral Primary Division.—Sterno-mastoideus, sterno-hyoideus, sterno-thyroideus, omo-hyoideus (especially anterior belly,) rectus lateralis, rectus antiquus minor, genio-hyoideus and thyrohyoideus.

IIND CERVICAL NERVE. (Plate 3, figs. 2, 4, 6; Plate 5, figs. 18, 19, 20, 21, and figs. 4, 5, and 6 in text, also sketch furnished to Dr. HEAD's paper, 'Brain,' 1894.)

The anterior boundary of the skin-field of this nerve has been delimited in six individuals; the posterior in five individuals.

Anterior Border. (Fig. 6.)

Example.—*M. rhesus.* Large female, not very young. At 11 A.M., the left Vth cranial nerve cut in the middle cranial fossa proximal to the Gasserian ganglion. At 9.30 P.M. "the anterior boundary of the field of response starts from the mid-

* A. FRORIEP and W. BECK, *loc. cit.*

dorsal line of the scalp at a point 3 centims. behind the supra-orbital ridge. The boundary runs thence in an almost rectilinear course transversely outwards to a point somewhat above and considerably in front of the top of the root of the pinna. From that point it begins to slope forwards, passing about midway between the outer edge of the orbit and the root of the pinna. In front of the tragus it lies 23 millims. distant from that. It cuts a line drawn from the root of the pinna to the angle of the mouth just about midway between those two points, and then sloping more abruptly forward, it passes about 15 millims. behind the angle of the mouth. It winds round the lower edge of the horizontal ramus of the jaw and

Fig. 6.

Anterior border of IInd cervical. Lines obtained on April 19, 1893 and April 13, 1893 compared.

reaches the mid-ventral line of the neck at a point a little in front of a vertical dropped from the angle of the mouth."

"The crossed overlap of the Vth cranial on the face and tongue is very slight indeed, but the crossed overlap of the IInd cervical, both on scalp and under chin, is considerable."

Posterior Border.

Example.—M. rhesus. Female, not young. At 9.30 A.M. the dorsal (sensory) roots of the IIIrd, IVth, Vth, VIIth, and VIIIth cervical and of Ist and IInd thoracic nerves of the right side severed in the vertebral canal. At 4.45 the final delimitation of the border of the upper field of response (IInd cervical) completed.

"The boundary starts from the mid-dorsal line of the neck at a point 1·5 centims. below the external occipital protuberance, and at a level about 1 centim. below the level of the lowest point of the root of the pinna. It slopes outwards and passes 2 centims. below the root of the pinna. It runs just below and behind the angle of the lower jaw. It meets the ventral crossed overlap of the opposite side a few millims. below the lower edge of the cricoid cartilage."

Variation.

In one adult female the IInd cervical skin-field reached in its ventral part further forward than in the other observations. The anterior border in the exceptional instance approached to within 7 millims. of the angle of the mouth, and sloping nearly horizontally along the lower edge of the jaw, turned under it and finally met the mid-ventral line only some 3 millims. behind the symphysis of the lower jaw. In Monkeys there is no mental eminence, but the position of the line is such as to suggest that in Man the skin-field of the IInd cervical will sometimes include the point of the chin, but will usually fall just short of that.

Ventral Primary Division of IInd Cervical Nerve.

When the dorsal primary division of the nerve has been severed at its origin from the trunk of the entire nerve, the change produced in the shape and extent of the skin-field is that instead of the field reaching the mid-dorsal line it stops short some centimetres above the root of the ear. The point where it stops short is about one-third of the way from the upper border of the root of the ear to the middle line of the scalp. The field is thus separated from the mid-dorsal line by a not very wide gap, and the lateral boundary of the gap is a line which runs parallel with the mid-dorsal. This line is the dorsal border of the skin-field of the ventral primary division of the nerve, and it joins the anterior and posterior borders of the skin-field at angles which approach very closely indeed to right angles. The skin-field of the ventral primary division covers quite four-fifths of the skin-field of the entire nerve.

Motor Distribution.

I have examined the distribution of the motor root of the IInd cervical nerve by mechanical and faradic excitation, and by faradic excitation of the separate dorsal and ventral divisions, in four individuals. My results are as follows, and showed no marked individual variation.

Dorsal Primary Division.—Cervicalis ascendens, trapezius, complexus, splenius, inferior obliquus, trachelo-mastoideus.

Ventral Primary Division.—Longus colli, sterno-mastoideus, rectus anticus major. Infra-hyoid muscles, viz., omo-hyoideus (chiefly posterior belly), genio-hyoideus, sterno-hyoideus, sterno-thyroideus, thyro-hyoideus.

IIIRD CERVICAL NERVE. (Plate 3, figs. 7 and 8; Plate 4, figs. 10, 13, 14; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, p. 66, and sketch furnished to Dr. HEAD's paper, 'Brain,' *loc. cit.*)

The anterior border of this skin-field has been observed in two individuals, the posterior border in six individuals.

Anterior Border.

Example.—M. rhesus, young ♀. The Vth cranial and the IInd cervical nerves cut inside the dura mater at 10.30 A.M. Final examination of the upper edge of the field of the IIIrd at 5.30 P.M.

"The upper edge of the field of response starts from the mid-dorsal line on the scalp at a point about 1 centim. behind halfway between the bregma and the lambda; it runs down to the back of the root of the pinna about 5 centims. from the top of the root; it turns over the upper edge of the pinna not far from the root, and then descends on the helix and in front of the tragus to reach the outer face of the vertical ramus of the lower jaw; along this it descends parallel with and slightly in front of the posterior edge of the ramus. It then bends forward in front of the angle of the jaw and slopes down the horizontal ramus of it to leave its lower edge and reach the mid-ventral line distinctly above the thyroid cartilage."

Posterior Border.

Example.—M. rhesus, ♀. At 11.20 A.M. the posterior roots of the IVth, Vth, VIth, VIIth, VIIIth cervical and Ist and IInd thoracic nerves divided inside the vertebral canal. At 5.15 P.M. the lower border of the IIIrd cervical finally delimited.

"The upper field of response has the following boundary: from the mid-dorsal line decidedly below the level of a line joining the lowest points of the roots of the two pinnæ, and thence outwards and slightly downwards for a distance of 2 centims. The line then turns more steeply downward well behind the posterior edge of the acromial end of the clavicle to strike the spine of the scapula just at the root of the acromion. It then turns forward over the outer end of the clavicle and again retires, thus making an angular notch, and reaching the top of the great tuberosity of the humerus. Finally it passes fairly horizontally inward well below the clavicle on the pectoral muscle, and reaches the ventral crosslap just above the junction of the 2nd costal cartilage with the sternum."

Variation.

The level of the posterior border at the mid-dorsal line is sometimes distinctly below the point found in the above experiment, but once it was on a level exactly with the line between the lowest points of the roots of the pinnæ. On two occasions instead of running well below the clavicle the line just followed the lower border of the clavicle. On one occasion the ventral end of the line passed between the 1st and 2nd cartilages somewhat nearer the second. The little notch in the border, close to the acromio-clavicular joint, was a constant feature of the field in all the experiments.

Muscular Distribution.

Examined in four individuals.

Dorsal primary division:—Complexus, splenius, trachelo-mastoideus, trapezius, cervicalis ascendens, transversi spinales.

Ventral primary division:—Longus colli, rectus antiquus major, levator anguli scapulæ; omo-hyoideus, post. belly; sterno-hyoideus, lower part.

IVTH CERVICAL NERVE. (Plate 3, fig. 3; Plate 4, figs. 9, 15, 16; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, pp. 66, 67, and sketch furnished to Dr. HEAD's paper, 'Brain,' *loc. cit.*)

The anterier border of this skin-field has been delimited in three individuals; the posterior border has been delimited in five individuals, but the two borders have not been delimited together in one and the same individual.

Anterior Border.

Example.—M. rhesus. Female, young. The Ist, IInd, and IIIrd cervical nerves of the right side severed in the vertebral canal, but outside the dura mater, at 10 A.M. "The anterior edge of the lower field of response (that of the IVth cervical nerve) can be traced from the mid-dorsal line of the scalp at a point corresponding with the lambda, that is, about 1 centim. above the external occipital protuberance. It sweeps outward at first horizontally to pass close (·5 centim.) behind the root of the pinna. It runs about ·5 centim. behind the vertical ramus of the jaw and meets the mid-ventral line on the neck at the level of the cricoid cartilage or a little above that."

Posterior Border.

Example.—M. rhesus. ♂, very young. At 10 A.M. the posterior roots of the Vth, VIth, VIIth cervical, and of the Ist, IInd, IIIrd, IVth, and Vth thoracic nerves of the right side severed. At 4.30 P.M. examination of the skin-fields completed.

"The upper field of response (IVth cervical) is bounded below by a line which starts from the mid-dorsal line of the body, about on a level with the upper end of the vertebral border of the scapula, and from these slopes down to meet the vertebral border at the root of the spinous process. Thence the line slopes down on the infra-spinous fossa, and recurves upward again, passing over the axillary border of the scapula, midway between the acromion process and the inferior angle. It then descends the arm below the prominence caused by the deltoid muscle and passes down the outer face of the arm in the groove between the muscular masses of the triceps and the flexors of the elbow. The line finally reaches a point as far as midway, or rather below midway, between the tip of the acromion and the angle of flexure of the elbow. From this point the line turns abruptly inward over the biceps, and, in so doing, recurves slightly toward the top of the shoulder. Before quite reaching the middle of the anterior surface of the biceps it slopes downward again and reaches a point on the inner aspect of the prominence caused by that muscle and nearly three quarters down the arm. Thence it turns upward again on the coraco-brachialis, and runs under the pectoral fold and then winds over the edge of that fold to attain the ventral crossed overlap of the skin-fields of the left side at a point about 1·5 centims. above the nipple, and just below the 3rd costal cartilage.

"The ventral crossed overlap is a full centim."

Motor Distribution.

Examined in four individuals.

The dorsal primary division supplied :—Complexus, splenius, trachelo-mastoideus, cervicalis ascendens, transverso-spinales.

The ventral primary division supplied :—Levator scapulæ, longus colli, levator claviculæ, scalenus medius, trapezius, subclavius. In three individuals the front, especially sternal, portion of the diaphragm. In one experiment this was examined by degeneration, the degeneration in the ventral division of the phrenic nerve on the diaphragm was much heavier than in the dorsal division.

Vth CERVICAL NERVE. (Plate 3, fig. 4; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, pp. 66, 67.)

1. *Sensory Root.*

The anterior border of the skin-field of this nerve has been delimited in two experiments; the posterior border in three experiments. In three individuals the entire field has been completely delimited.

Anterior border :—

Example. M. rhesus, ♀, young. At 11 A.M. the Ist, IInd, IIIrd and IVth cervical nerves of the right side cut inside the vertebral canal. At 5.30 the final delimitation of the border of the Vth cervical completed.

"The boundary line starts from the mid-dorsal line about 3·5 centims. below the lambda, that is, superficial to about the 3rd cervical vertebra; from that point it sweeps laterally in a descending line considerably below the mastoid process. It passes downward behind the sterno-mastoid muscle to the clavicle at the junction of the middle and outer thirds of that bone, and it then turns horizontally inward along the clavicle to reach the crossed overlap of the skin-fields of the nerves of the opposite side of the body at a distance of about 8 millims. from the mid-ventral line."

Entire field:—

Example. M. rhesus, ♂. At 9.30 A.M. the posterior roots of the IIIrd, IVth, VIth, VIIth and VIIIth cervical nerves and of the Ist, IInd and IIIrd thoracic nerves severed. Final determination of the isolated field of response at 4 P.M.

"The field is bounded by a line which starts from near the mid-dorsal line above the scapula and on the trapezius muscle. It runs outward in a direction roughly parallel with and well above the origin of the deltoid muscle. Continuing this course, it winds round the anterior border of the trapezius, curves inwards a little along the hollow between the clavicular portions of the trapezius and sterno-mastoid muscles, winds inwards across the front of the clavicular origin of the sterno-mastoid, and reaches the mid-ventral line. The posterior edge of the field starts on the sternum at the level of the third costal interspace, it then tends laterally, lying about two fingers' breadths above the nipple, and attains the lateral edge of the pectoralis muscle after a horizontal course. The edge of the pectoralis it follows to the edge of the deltoid, and it then runs along the top of the bicipital swelling, rather nearer to the ulnar than to the radial edge of the muscle. It enters the forearm over the tendon of the biceps and sweeps down the supinator longus prominence, recurving on itself about half-way down the forearm. The field thus includes a tongue-shaped area of the forearm, fairly covering the belly of the *supinator longus.* The boundary returns up the arm, passing in front of the outer condyle and up the outer face of the limb along the groove between flexors and extensors. It follows the posterior border of deltoid approximately; it crosses the spinous process of the scapula near the base of that, and gets to the mid-dorsal line of the trunk opposite the spine of the 1st thoracic vertebra; it slopes suddenly upward near the mid-dorsal line, as if it only partially attained to that line."

Posterior border:—

Example. M. rhesus, female. At 9.30 A.M. the posterior roots of the VIth, VIIth and VIIIth cervical nerves, and of the Ist, IInd and IIIrd thoracic nerves severed in the spinal canal. Two days later the lower border of the upper field of response finally determined. It agreed with the delimitation on evening of first day. It descended the forearm for barely two centims.; the part of the forearm it occupied lay well in front of the external condyle on the crest of *supinator longus* prominence.

Variation:—

A considerable amount was met with in the observations on this field. In one individual the anterior border was at least two centims. lower than in the others, and the evidence that the posterior border of the field did actually attain the mid-ventral line was not convincing.

2. *Motor Root.* Vth cervical. (*See* Conspectus, p. 119 *infra.*)

The method of examination adopted for the motor root was, as above explained, section of the motor roots adjoining that to be examined, then, after a lapse of at least 14 days, excitation with the faradic current of the remaining sound root in the vertebral canal, and of the various nerve-trunks composing the brachial plexus.

On the motor root of the Vth cervical nerve four such experiments were carried out, one on *M. sinicus*, the rest on *M. rhesus*.

The root was found to be distributed to the following muscles:—

Dorsal primary division: *erector spinæ* and *transverso-spinales*.

Ventral primary division:

- *longus colli*.
- *rhomboidei*.
- *levator anguli scapulæ*.
- *serratus magnus*.
- *pectoralis major* (clavicular portion only).
- *deltoideus* (clavicular and acromial portions).
- *teres minor*.
- *supraspinatus*.
- *infraspinatus*.
- *subscapularis*.
- *scalenus medius*.
- *bicep* (both heads).
- *brachialis anticus*.
- *coraco-brachialis* (slightly only).
- *supinator longus* (feebly), and *brevis* (very feebly).
- *extensor carpi radialis longior* (feebly; in one experiment not at all).
- *extensor carpi radialis brevior* (feebly; in two experiments not at all).
- *diaphragma*: degeneration heavy in both sternal (ventral) and vertebral (dorsal) divisions of the phrenic on diaphragm.
- *subclavius*.

VIth CERVICAL NERVE. (Plate 3, figs. 5, 6; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, pp. 66, 67.)

1. *Sensory Root.*

This skin-field has been delimited completely in four individuals, and incompletely in two more.

Example.—*M. rhesus.* ♀, young. At 9 A.M. the posterior roots of the IIIrd, IVth, Vth, VIIth and VIIIth cervical, and of the Ist, IInd and IIIrd thoracic nerves were severed in the vertebral canal. The isolated field of response, due to the intact VIth cervical root, was finally delimited about 5 P.M.

"The field of response is limited by a line which starts from a point on the infraspinous fossa of the scapula near the edge of the deltoid muscle. The line crosses the lateral part of the infraspinous fossa obliquely and turns down the arm behind the posterior border of the deltoid muscle. It descends the arm lengthwise, well on the triceps side of the furrow, between the masses of the extensors and flexors of the elbow. It enters the forearm close behind the outer condyle, and thence passes in an almost straight line to reach the radial side of the index finger, where on the proximal phalanx it recurves. The line returns across the palm to the fore-arm over about the middle of the thenar eminence; it crosses the wrist on the radial side of the lower radio-ulnar joint. On the flexor aspect of the forearm it ascends close to the ulnar side of the prominence made by the supinators of the wrist and long extensors of the fingers. It crosses the flexure of the elbow about the middle of it, and climbs the prominence over the flexors of the elbow somewhat to the ulnar side of the middle line of the biceps. Close above the junction of the limb with the trunk the line turns outward and downward, and sweeping below and round the deltoid muscle reaches the spot on the infraspinous fossa whence it was traced."

Variation.

In the first experiment the field traced was closely similar to the above; in a third experiment it did not appear to extend lower than the styloid process of the radius, and I convinced myself it did not include the thumb, for the observation was repeated many times in the course of 24 days. When the animal was finally examined, electrical excitation of the central end of the musculo-cutaneous nerve, about 3 inches below the elbow, elicited smart reflexes. In a fourth individual nearly the whole length of the radial side of the index finger was included in the field.

There must, therefore, be a considerable degree of variation in the extent to which this nerve contributes to the sensation of the skin of the hand. The thumb, and even one half of the index finger, in some individuals, enter into the composition of the field, but in some they do not.

2. *Motor Root.* VIth cervical. (*See* Conspectus, p. 119 *infra.*)

Three experiments, all on *Macacus rhesus*, by the combined degeneration and excitation method as explained above (p. 52).

The distribution of the root was found to include the following muscles :—

The dorsal primary division innervated the following, as tested by experimental excitation :—

erector spinæ.
transverso-spinales.

The ventral primary division as given below :—

scaleni (not always).
teres major.
teres minor.
rhomboidei.
serratus magnus.
pectoralis major.
deltoideus (apparently the *whole* of the muscle).
supraspinatus.
infraspinatus.
subscapularis.
biceps caput longum.
biceps caput breve.
brachialis anticus.
coraco-brachialis.
supinator longus.
supinator brevis.
extensor carpi radialis longior.
extensor carpi radialis brevior (slightly).
pronator radii teres (slightly).
flexor carpi radialis (slightly).
latissimus dorsi.
diaphragma (especially the portions nearer the vertebral column and lateral part attached to lowest ribs).
longus colli.
triceps.

In one experiment, a part of the outer head of *triceps* contracted feebly but distinctly.

In two experiments, the distribution was further examined by tracing *microscopically* the Wallerian degeneration in the nerve twigs of the limb twenty days subsequent to section of the motor root of the inside of the vertebral canal.

Degeneration was found in the nerve twigs to the following muscles :—*

	deltoideus.
	teres major.
	subclavius.
	teres minor.
	subscapularis.
	supraspinatus.
	infraspinatus.
	biceps.
	latissimus dorsi.
	coraco-brachialis.
	brachialis anticus.
	supinator longus.
	extensor carpi radialis longior.
	extensor carpi radialis brevior.
In both experiments	*triceps,* in outer and inner heads (but slight degeneration only).
	supinator brevis.
In one experiment, not in both	*flexor carpi ulnaris* (slight degeneration).
In both experiments	*extensor communis digitorum* (a few fibres only).
In one experiment, not in both	*extensor longus pollicis* (a few fibres only). *extensor ossis metacarpi pollicis* (six fibres only). *flexor longus pollicis* (a few fibres only).

It will be seen that the five last mentioned muscles were not noticed by the previous method to respond to the excitation of the VIth cervical root; the teasing method was carried out only after the examination made by the excitation method above described, and it is possible that if its results had been known, and particularly minute attention paid to the above muscles, some trace of contraction might have been found; but it seems clear that, if detectible, it was so slight as to have escaped a careful search. I am, therefore, inclined to consider the amplification of the list obtained by the purely microscopical method of teasing to be explicable not by individual variation, but by a greater delicacy of the "teasing" than of the previous method. Allowing twenty muscle fibres to each neuron, the six neurons contributed by the VIth cervical segment to the motor innervation of the extensor ossis metacarpi pollicis might—especially if, as is most probable,† scattered about the thickness of the muscle—under excitation evoke no *appreciable* contraction in the muscle.

* The serratus magnus and pectoralis major were not included in the search by teasing, partly on account of their size, partly because the labour was believed to be superfluous.

† SHERRINGTON, "Lumbosacral plexus," 'Journ. of Physiol.,' vol. 13, 1892, p. 751.

My experiments on this nerve bear out the statement by FORGUE and LANNEGRACE,* that the hinder parts of the diaphragm is supplied by the VIth cervical nerve; so also my degeneration obtained of the IVth cervical, bear them out that that root supplies the front of the diaphragm; but the degenerations show that there is much intermingling of the two nerves, both with each other and with the Vth in their distribution both to back and front.

My observations on this nerve bear out THORBURN's† statement, based on clinical observation, that the nerve supplies the teres major, latissimus dorsi, sternal portion of pectoralis major, and the triceps—a statement contrary to FORGUE and LANNEGRACE's‡ experiments.

THE DIAPHRAGM. The degeneration in the phrenic after section of VIth cervical in *Macacus* is heavy. Of the two main divisions into which the phrenic divides on reaching the diaphragm, the degeneration is considerably greater in that (dorsal) which turns backward toward the vertebral column than in that which turns forward (ventral).

Degenerated fibres I found in considerable numbers in the phrenic twenty days after section of the motor root of the IVth cervical; but in this instance the amount of degeneration was greater in the division of the nerve which turned forward toward the sternal border of the muscle than in that turning backward. The diaphragm in all my experiments proved to be a trimeric muscle, that is to say, drew its innervation from a series of three consecutive spinal nerves, resembling in this character the majority of the limb muscles. The elements of the individual metameres are also, as in the limb muscles, much commingled and not strictly territorially arranged.

VIIth CERVICAL NERVE. (Plate 3, figs. 7 and 8; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, pp. 66, 67; and figs. 7, 8, pp. 102, 103.)

This skin-field has been delimited completely in four individuals and incompletely in a fifth.

Example.—*M. rhesus.* ♀, young. At 11.15 A.M. the posterior roots of the IIIrd, IVth, Vth, VIth and VIIIth cervical, and of the Ist, IInd, IIIrd, IVth, Vth and VIth thoracic nerves of the right side divided. The isolated field of response due to the VIIth cervical being intact, was finally delimited at 4.30 P.M.

"The field of response is limited by a line which is traceable from the radial side of the cleft between the 3rd and 4th digits, and runs along the palm on the radial edge of the main longitudinal furrow. From the palm it takes an almost rectilinear course ascending the flexor aspect of the forearm along the hollow between the flexor and the supinator groups of muscles. It attains the radial side of the biceps tendon and then mounts the swelling prominence of the biceps muscle; at first it fairly

* 'Compt. Rend.' vol. 98, p. 829.

† 'Brain,' xxxvi., p. 510; xliii., p. 289.

‡ *Loc. cit.*

bisects the surface of this prominence longitudinally, but higher up the line tends outward and ascends over the insertion of the deltoid muscle, and then recurves abruptly downward below the insertion of the deltoid and again bends upward behind the deltoid : once more abruptly recurving it descends and follows the groove between extensors and flexors of elbow-joint. The line enters the extensor surface of the forearm closely behind the head of the radius and well in front of the olecranon process of the ulna. It runs down the back of the forearm nearer the ulnar than the radial edge, especially in the distal half of the region. The line enters the dorsal surface of the hand by passing over the joint between ulna and radius, and runs to the mid-point of the knuckle of the ring-finger and down the back of the proximal phalanx of that finger for a short distance. Finally, the line turns abruptly outward to reach the cleft between the middle and the ring fingers, and attains there the point from which it was traced."

The individual variation met with in examining this field has been slight, but in two cases the field included all but the ulnar face of the ring-finger. In another (fig. 7, p. 102) it included part of ring-finger.

2. *Motor Root.* VIIth root. (*See* Conspectus, p. 119 *infra.*)

Three experiments, two on *Macacus rhesus*, one on *Macacus sinicus;* all by degeneration method.

Dorsal primary division : *erector spinæ* and *transverso-spinales.*

Ventral primary division:

- *scaleni.*
- *serratus magnus.*
- *pectoralis major* (the whole muscle, apparently).
- *pectoralis minor* (less vigorously than *p. major*).
- *deltoideus* (especially the portion from the scapular spine).
- *longus colli.*
- *latissimus dorsi.*
- *triceps* (especially the long and outer heads) *anconeus.*
- *teres major.*
- *subscapularis.*
- *infraspinatus.*
- *coraco-brachialis.*
- *supinator longus.*
- *extensor carpi radialis longior.*
- *extensor carpi radialis brevior.*
- *flexor sublimis digitorum.*
- *flexor profundus digitorum.*
- *flexor carpi radialis.*
- *pronator radii teres.*

Ventral primary division—*cont.*
- *extensor communis digitorum*, *extensor carpi ulnaris*, *extensor ossis metacarpi pollicis*, *extensor longus pollicis*, *flexor brevis pollicis* (superficial head only) — feebly, but distinctly.
- *biceps*, *brachialis anticus*, *flexor carpi ulnaris*, *flexor longus pollicis*, *supinator brevis* — feebly ; in one experiment not at all.

In one experiment further the degeneration method was completed by teasing nerve-twigs to muscles, and the following muscular branches revealed degenerate motor fibres, the right hand VIIth cervical nerve having been severed in the vertebral canal twenty days previously.

Supraspinatus.×
infraspinatus.
pectoralis minor.
biceps.
supinator longus.
extensor carpi radialis longior.
extensor carpi radialis brevior.
pronator radii teres.
triceps (outer head).
flexor carpi radialis.
palmaris longus.×
flexor carpi ulnaris.
extensor communis digitorum.
extensor longus pollicis.
extensor brevis pollicis.×
extensor ossis metacarpi pollicis.
extensor indicis.×
superficial short muscles of thumb. Lumbricals (2) and interossei (2).
flexor sublimis digitorum.
flexor profundus digitorum.
extensor carpi ulnaris.
extensor minimi digiti.×
pronator quadratus× (two degenerated fibres).
supinator brevis (two degenerated fibres).

The six muscles marked with a cross have, therefore, to be added to those given in the previous list in order to complete the motor distribution of the VIIth cervical segment.

In this experiment not a single degenerate nerve-fibre was detected in the cervical sympathetic trunk.

The phrenic trunk contained no degeneration after section of this root.

VIIIth Cervical Nerve. (Plate 3, fig. 3; Plate 4, figs. 9, 10, 11, 12, 13, 14, 15; Plate 5, figs. 18, 19, 21. Figs. 4 and 5, pp. 66, 67.)

This skin-field has been delimited completely in three individuals, incompletely in a fourth and fifth.

Example.—M. rhesus. ♂ strong, young. At 10 A.M. The Vth, VIth and VIIth cervical, and the Ist, IInd, IIIrd, IVth and Vth thoracic roots of the right side severed in the vertebral canal.

An isolated *field of response*, that supplied by 8th cervical root, was finally delimited at 4.30 P.M. This field was contained within the following boundary. From a point about one quarter the way up the outer edge of the upper arm in the furrow between the biceps and triceps muscles the boundary slopes abruptly back across the triceps for about 2 centims., and then recurves at less than a right angle to pass downward between the olecranon and the outer condyle of the humerus and gain the forearm. It descends the outer side of the extensor surface of the forearm for about one-third the way to the wrist, and then slants toward the ulnar side and attains the ulnar edge about one-third up the forearm. It slopes round as far as the flexor aspect of the ulnar edge and then sharply recurves on itself, tending upward and outward across the face of the flexor aspect of the forearm to a point about two-fifths up the flexor aspect of the forearm and midway between its radial and ulnar borders. Thence the line of boundary returns and descends just to the ulnar side of the pronator longus tendon. Close above the wrist it slopes outward and attains a point one centim. above the styloid process of the radius; from that the line runs up the forearm on the outer face of the prominence caused by the prominence of the group of supinator muscles, and it ascends finally the furrow between biceps and triceps to the point whence it was originally traced."

The agreement between the limits of this field in the individuals observed has been singularly close; the discrepancies have been too small to be clearly outside the limits of errors inherent in the experimental testing of the skin. The analogy between the cutaneous distribution of the VIIIth cervical in the fore limb, and of the VIth lumbar (Vth lumbar of man) in the hind limb is curiously great. Each supplies the skin covering the whole free apex of the limb to which it belongs, and each has anterior to it a nerve-root which supplies the skin of only the anterior side of the free apex of the limb, and each has next behind it a nerve-root that supplies the skin of only the posterior portion of the free apex of the limb.

Although this (VIIIth cervical) skin-field extends further along the radial edge of the forearm than along the ulnar edge, it was noted in each of the experiments made that when the "contracted field" was examined, the reply from the pollex was much less brisk than from the fifth digit; also, the reply from the radial side of the forearm was gradually developed under "extension of the field." The centre of the field in the hand lies, therefore, in all probability nearer to the ulnar than to the radial border.

2. *Motor Root.* VIIIth cervical. (*See* Conspectus, p. 119 *infra.*)

Three experiments, all on *Macacus rhesus,* and by combined degeneration and excitation method as above.

The root is distributed to the following muscles :—

scaleni.
pectoralis major.
pectoralis minor.
triceps (all three heads, especially, perhaps, to the long head).
latissimus dorsi (especially to a portion near the humeral attachment).
extensor carpi ulnaris.
extensor communis digitorum.
extensor ossis metacarpi pollicis.
extensor longus pollicis.
extensor brevis pollicis.
extensor indicis.
extensor minimi digiti.
flexor carpi radialis.
flexor carpi ulnaris.
flexor sublimis digitorum.
flexor profundus digitorum.
flexor longus pollicis.
palmaris longus.
pronator quadratus.
the intrinsic muscles of the hand, including the interossei.
teres major—in one experiment only.
coraco-brachialis—in one experiment only.

In two further experiments the VIIIth cervical ventral (motor) root having been severed twenty days previously, degenerate fibres were found in nerves to the following muscles :—

flexor carpi radialis.
triceps, outer and middle heads and anconeus.
palmaris longus.
flexor carpi ulnaris.
extensor communis digitorum.
flexor longus pollicis.
extensor longus pollicis.
extensor brevis pollicis.
extensor indicis.
superficial short muscles of thumb.
flexor sublimis digitorum.
flexor profundus digitorum.
pronator quadratus.
extensor carpi ulnaris.
extensor ossis metacarpi pollicis.
extensor minimi digiti.
deep set of the short muscles of the thumb.
short muscles of little finger.
1st, 2nd, 3rd lumbricales.
1st, 2nd, 3rd palmar interossei.
all the dorsal interossei.

extensor carpi radialis brevior pronator radii teres	A few degenerate fibres were present in one of the experiments, but were absent in the other.

IVth palmar interosseus muscle—it was doubtful if any degenerate fibres existed in the nerve of this muscle in the experiment in which some were present in the nerve to extensor carpi radialis brevior—but in the other experiment there were some undoubtedly present.

In each of these experiments degenerate fibres existed in the cervical sympathetic —in the former case two fibres, in the latter five; the degenerate fibres were small myelinate (less than $3{\cdot}5\ \mu$).

When the motor root of this nerve has been completely destroyed by degeneration a number of perfectly sound myelinate fibres are still to be found in the small *primary dorsal division* of it, although that division supplies no cutaneous branch. The sensory fibres in this division must be destined for muscles, ligaments, and connective tissue endings. The motor fibres in the division supply the *erector spinæ* and *transverso-spinales*.

IXTH NERVE OR IST THORACIC NERVE. (Plate 4, figs. 16, 17; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, p. 66, 67, and figs. 7, 8, pp. 102, 103.)

1. *Sensory Root.* Distribution to Skin.

Example.—*M. rhesus*, ♀. At 9.30 A.M., the posterior roots of the Vth, VIth, VIIth and VIIIth cervical and of the IInd, IIIrd and IVth thoracic nerves of right side cut in the spinal canal. At 6 P.M. the skin-field of the Ist thoracic was finally determined.

"The field of response isolated is limited by a line traceable as follows:—From a point in the flexure of the elbow superficial to the biceps tendon and thence down the front of the forearm and across the wrist a little to the radial side of the inferior radio-ulnar articulation along the palm in a straight line to the cleft between middle and ring fingers, thence along the radial side of the ring-finger as far as the last phalanx, on the radial face of which it recurves and runs back along the dorsal face of the middle and proximal phalanges to the hand. On the dorsum of the hand it takes a fairly straight course, passes over the back of the inferior radio-ulnar joint, and climbs the forearm along the extensor aspect to the external condyle of the humerus, and passes a centim. or more above that. The line then makes a curious and characteristic rectangular bend, winding round the olecranon to the inner condyle of the humerus, and then tending up the arm along the axillary face of the coraco-brachialis, and making for a point just below the insertion of the deltoid. The line, when it has nearly reached the deltoid insertion, recurves and then passes down the skin over the biceps to the point whence it was traced; it thus includes a tongue-shaped area pointed upwards on the lower part of the flexor and axillary surface of the upper arm."

Varieties.—In one individual a little of the ulnar side of the middle finger and the whole of the ring-finger, and in another individual (figs. 7, 8, pp. 102, 103 in text) the whole of the ring and middle fingers and a piece of the ulnar side of the root of the index, were included in the field of the Ist thoracic. This is not usual.

This skin-field has been delimited in eight individuals—in five for the present paper, in three for my previous communication.

I am inclined to think that on this skin-field, which seems a little post-fixed as compared with the human, rests some of the best evidence that the human brachial plexus, and therefore the skin and musculature of the arm of Man are somewhat prefixed as compared with *Macacus*. In Man the Ist thoracic sends a branch back to join the IInd thoracic (cutaneous), but it does not do so in the Macaques I have dissected.

2. *Motor Root. Ist Thoracic.* (*See* Conspectus, p. 119 *infra*.)

Two experiments, both by degeneration method: one performed on *Macacus rhesus*, one on *Macacus sinicus*. The muscular distribution was in this way found to include the following:—

scaleni.
pectoralis major (lower body only).
pectoralis minor.
triceps (inner head, long head less).
latissimus dorsi (in part).
serratus posticus superior.
palmaris longus.
flexor carpi ulnaris.
flexor profundus digitorum.
flexor sublimis digitorum.
flexor longus pollicis.
pronator quadratus.
extensor ossis metacarpi pollicis.
extensor longus pollicis.
extensor brevis pollicis.
extensor communis digitorum.
extensor indicis.
extensor minimi digiti.
extensor carpi ulnaris.
intrinsic muscles of the hand including the interrossei.

A further examination of the distribution of this motor root was carried out as before by degeneration and teasing nerve-trunks. Degenerate nerve-fibres were traced to the following muscles :—

flexor carpi radialis.
palmaris longus.
extensor communis digitorum.
flexor profundus digitorum.
flexor sublimis digitorum.
pronator quadratus.
extensor carpi ulnaris.
extensor indicis (not always).
extensor internodii pollicis (not always).
extensor minimi digiti.
superficial short muscles of the thumb.
deep short muscles of the thumb.
short muscles of little finger.
1st, 2nd and 3rd lumbricales.
all the palmar } interossei { The amount of degeneration was greater in the
all the dorsal } interossei { IVth palmar interosseus than in the Ist.

In this experiment 73 degenerate fibres were present in the cervical sympathetic —fine myelinated all of them.

After this motor root has been destroyed by degeneration, a considerable number of perfectly sound nerve-fibres still persist in the first intercostal nerve. This latter must therefore contain a number of afferent nerve-fibres, although in the Monkey it does not give any lateral or other cutaneous branch—at least I have found none. In the same way the small dorsal primary division of this nerve is found to contain a number of fibres from the spinal root-ganglion although it gives off no cutaneous branch. The motor fibres in the small *posterior primary division* innervate the *erector-spinæ*, *levator costæ*, and *transverso-spinales*.

XTH NERVE OR IIND THORACIC NERVE. (Plate 3, figs. 4, 6; Plate 5, figs. 18, 19, 20, 21. Figs. 4 and 5 in text, pp. 66, 67; also Plate 42, fig. 1, of my previous paper, 'Phil. Trans.,' B, 1892.)

1. *Sensory Root. Distribution to Skin.*

Example.—M. rhesus. ♀. At 10 A.M., the posterior roots of the IIIrd, IVth, Vth, VIth, VIIth and VIIIth cervical, and of the Ist, IIIrd, IVth and Vth thoracic nerves of the right side severed; at 5 P.M., the skin-field of IInd thoracic nerve finally delimited.

"The isolated field of response is limited by a line which runs as follows:—It starts at a point one-third down the forearm, at the junction of the ulnar and flexor surfaces: it from there slopes upward across the root of the olecranon, and along the space between olecranon and inner condyle. It passes up the upper arm along the middle of the posterior aspect of it, on the surface of the triceps behind the biceps, and close behind the deltoid muscle. It meets the spine of the scapula near its acromial end, and at once returns to sweep into axilla and recurve upward once more and wind the pectoral fold to the front of the chest on pectoralis. It then retires again, and comes down the outer aspect of the arm. It passes just in front of the outer condyle of the humerus, and down the extensor face of the forearm, sloping towards the head of the ulna, and above that recurves, to pass upwards and attain the point whence it was originally traced. It therefore reaches a little more than half way down the forearm, and approaches the wrist most nearly in the skin over the ulnar border of the forearm."

2. *Motor Root. IInd Thoracic Nerve.* (*See* Conspectus, p. 119 *infra.*)

I have never, in *Macacus*, found wanting a distinct contribution from the IInd thoracic to the brachial plexus. I ascertained by degeneration experiments that this, which is too short to stimulate without some risk of escape of current, contains both motor and sensory fibres. In full accord with the distribution of the degeneration, excitation of the IInd thoracic motor root gives contraction of a number of hand muscles. W. KRAUSE, although he noted the presence of this branch in the Rabbit, did not discover its importance to the plexus. FORGUE and LANNEGRACE overlooked it altogether in Dog and Monkey. FERRIER and YEO (1884) were the first to demonstrate that it contributes to the hand: they describe it as supplying the *interossei* and evoking "interosseous flexion." In my own paper I noted instances in which it evoked flexion and pronation at wrist, as well as full flexion of the thumb and fingers, both in *M. rhesus* and in *sinicus*; also in *Cercopithecus* and in *Cynocephalus*. I have also seen slight flexion of the wrist as a willed movement in a Macaque in which the VIth, VIIth and VIIIth cervical and Ist thoracic roots had been cut through. In fact, it supplies flexor profundus, flexor sublimis, palmaris longus, pronator quadratus, as well as the muscles of the hand.

In all cases the *scaleni* (not *medius*) muscles contained degenerated nerve-fibres; as also, *viâ* the posterior primary division of the nerve, the *erector spinæ* and *transverso-spinales*.

Examined by the degeneration method and the teasing of muscle-nerves for detection of breaking down nerve-fibres, the following results were obtained in two Macaques:—

Experiment 1.

palmaris longus.
pronator quadratus.
flexor longus pollicis.
flexor sublimis digitorum.
flexor profundus digitorum.
deep short muscles of thumb.
all the lumbricales.
all the dorsal } interossei.
all the palmar }
short muscles of little finger.

Experiment 2.

flexor longus pollicis.
flexor sublimis digitorum.
flexor profundus digitorum.
deep short muscles of thumb.
short muscles of little finger.
all the lumbricales.
all the dorsal } interossei.
all the palmar }

The fact that after degeneration of the lowest four cervical and of the Ist thoracic nerves, excitation of the IInd thoracic or of the cords of brachial plexus still evokes a flexion of the wrist and of the digits, in which the terminal phalanges of the latter are flexed on the middle phalanges as well as these last on the proximal, might be taken to prove that the flexor profundus digitorum was in action, and therefore innervated by the IInd thoracic. The flexor profundus is, it is true, usually innervated in part by the IInd thoracic, but the above fact is not the proof of it. In Man the flexor profundus (perforans) is the flexor of the terminal phalanges on the middle phalanges, and the sublimis does not flex the former. In the Macaque both profundus and sublimis flex similarly the terminal and middle and proximal phalanges; if the middle phalanges are prevented from flexion (as presumably under action of the interossei and lumbricales), the sublimis cannot flex the terminal phalanx, although the profundus can. This action can be easily examined by pulling on the respective tendons in the Macaque.

In all the Macaques I have examined in reference to the point, the IInd thoracic innervates the hand not only *viâ* the ulnar nerve, but also *viâ* the median. HEPBURN has described that in Monkeys the ulnar gives a considerable branch to the median in the upper part of the forearm. It is through this that the above-described distribution takes place. Although present in the Macaque, I have never met with this forearm branch in *Cercocebus* nor in *Cynocephalus*. These latter forms do possess, however, the somewhat similar communication between external saphenous nerve and external plantar at the heel deep to the tendo Achillis, which I described and figured in my former paper in *Macacus*.* The contribution from ulnar to median contains cutaneous sensory fibres as well as motor efferent (see p. 107, fig. 11, p. 106, below). The communication between ulnar and median is normal in most Mammals.† In Man it occurs in 20 to 25 per cent. of individuals,‡ a fact which lends more interest to the physiological analysis of the communication as it exists in *Macacus*.

It will be noted that although the IInd thoracic nerve contributes to the innervation of the muscles of the hand and lower forearm, it does not contribute to the sensory innervation of any part of the skin of the hand, nor even to that of the lower part of the forearm. Also, although it supplies the muscles of the second intercostal space, the skin overlying the second intercostal space is not innervated by it. I have already pointed this out as a striking illustration of the want of real basis for the so-called "law" (VAN DER KOLK, HILTON), which states that muscles and their overlying integument are supplied by the *same* segmental nerves. The skin over the first and second intercostal spaces is in great part innervated from segments five and six, segments further headward than the source of innervation of the underlying muscles, *e.g.*, first intercostal space: muscles, Ist thoracic, skin, IVth cervical.

In concluding this section a few words are desirable regarding the comparison between the segmental anatomy of Man and of *Macacus* in this region. Beyond question the similarity between the two is almost minutely exact. The most salient point of difference appears in the motor distribution of the IInd thoracic root, which is not generally considered to contribute to the brachial plexus in Man. Its contribution is of almost universal occurrence in the animals used in the Laboratory. I have tested the point by dissection and stimulation in the Dog, Cat§, Horse, Rabbit, and Rat, as well as in Monkeys, and find it among the types examined of inconstant presence in the Cat and Dog only: it is more frequently absent in Cat than in Dog, and sometimes on one side only. That a communicating branch often passes in Man from IInd thoracic to Ist thoracic has been seen by CUNNINGHAM, who found it in 70 per cent. of the individuals examined. If the IInd thoracic does not really contribute to the

* 'Journal of Physiology,' vol. 13, p. 643, Plate 21, fig. 7.

† BARDELEBEN.

‡ QUAIN'S 'Anatomy,' vol. iii., part 2, p. 302. THANE, 1895.

§ My results on this point were demonstrated to the Physiological Society Feb. 13th, 1892. At that date Dr. Langley had already (Jan. 20th) sent in a paper to the Royal Society ("Origin of the Cervical and upper Thoracic Fibres of the Sympathetic." Read Feb. 18th. 'Phil. Trans.,' B, 1892) in which, as regards the Cat and Rabbit, results similar to my own had been arrived at. 10th July, 1897, C.S.S.).

human brachial plexus, the plexus of Man is prefixed as compared with that of the other types. Now in the Macaque the rectus capitis anticus major is supplied not from the Ist cervical root as in Man. The *Scaleni*, all three, are present in Macaque as in Man, but they receive a more posterior root supply than in Man, the upper two thoracic roots contributing to their innervation, whereas the IInd and IIIrd cervical roots do not contribute to them in *Macacus*, though they do so in Man. In the Macaque I have in one individual found the IIIrd cervical motor root innervating the diaphragm (ventral part), but in one instance only. Concordantly with this the VIth cervical in *Macacus* I have found to supply the diaphragm regularly (examination by degeneration and "teasing," as well as by excitation method). In a Macaque in which the VIIth right cervical nerve had been severed twelve days, I failed to discover degenerate fibres in the phrenic trunk. In Man the phrenic "arises mainly from the IVth nerve, also receiving in the majority of instances an additional root from either the IIIrd or the Vth nerve" (THANE). On the other hand, in his 'Anatomy of Domesticated Animals,' CHAUVEAU describes the phrenic as arising mainly from the VIth and VIIth nerves, with a subsidiary branch from the Vth. As judged by the root-constitution of the phrenic nerve, therefore, the muscles innervated by the brachial region of the cord are more prefixed in Man than in the other Mammalian types coming under observation, including Monkey. It may be, therefore, that in a certain number of human brachial plexuses the IInd thoracic does not contribute to the innervation of the hand muscles; and certainly in *Macacus* the amount of contribution by it varies, for I have in some individuals failed to evoke contraction of the deep flexor of the forearm through it, though this is often readily done. On the other hand again, it is possible that the segmental position of diaphragm (or rather of phrenic nerve) may vary independently of that of the musculature (or nerve-trunks) of the limb; but this supposition is not in harmony with the rule I found deducible from the lumbo-sacral plexus, viz., "the shifting up or down of the region of outflow along the cord applies to all the efferent fibres of that length"; in other words, although each muscle (nerve-trunk) is displaced absolutely, it is not displaced relatively to its neighbours. LANGLEY'S researches on the Sympathetic show that, to use my own nomenclature, the cervical sympathetic is more prefixed in the Cat and Dog than in the Rabbit; a fact in accord with the not infrequent absence of the contribution from IInd thoracic noted above in the Cat (and Dog). KLUMPKE'S conclusion from clinical data, that in Man the dilatators of the pupil emerge from cord *entirely* in the Ist thoracic root, is almost certainly not correct. We know of no type, including Monkey, in which the outflow of dilatators is limited to one root, and BRUN'S case shows that in Man some leave by a root lower than Ist thoracic. Yet KLUMPKE'S evidence makes it probable that they leave in man *chiefly* by Ist thoracic. If so, then the evidence from the sympathetic, and also from the phrenic, points to the nerves and muscles of this region in Man being prefixed, as compared with *Macacus* and the laboratory types. This fact may be remembered in connection with the reduction of sensory roots which seems to be in progress at the top of the neck; the ganglion of the hypoglossal, and that of the Ist cervical roots, both present in Ruminants, the latter present in the Cat and Rabbit, have both disappeared in *Macacus*, and in Man.

As to the spinal skin-fields of *Macacus* and of Man, clinical opportunities arise for observing some of the latter sufficiently to give ground for brief examination of the correspondence between the two. The opportunities of the bedside have afforded the basis for the admirable papers of THORBURN, HEAD, JAMES MACKENZIE, STARR, and KOCHER. In regard to the IVth cervical, STARR's determination of the posterior edge tallies closest in general level with that of *Macacus*; HEAD's determination in shape of contour, the curious double shoulder peak of *Macacus* appearing with fidelity in Man. In regard to the Vth cervical, there is close agreement between all the clinical observers and the experiments on *Macacus*; in the photograph of one of my experiments the posterior border of Macaque's skin-field must have agreed point for point with THORBURN's figure of that border; MACKENZIE's figure also gives almost exactly the same situation for it. In the clinical determination of the posterior border of VIth cervical the limit given it on the hand in BRUN's case agrees absolutely with that part of one of my photographs of *Macacus*. But, as stated above, I found frequent slight variation of this border in *Macacus*, and the more usual position of the border in *Macacus* is one agreeing accurately with WILLIAMSON's case, and with the right hand in HERTER's case. These cases go far to show that the agreement in this region between *Macacus* and Man is very close, extending even to details of individual variation. HEAD's upper patch—a deltoid patch—of the VIth cervical field is included quite identically by *Macacus*. As to the VIIth cervical, THORBURN's fig. 5, which he suggests is the VIIth cervical (of course, its posterior border only) closely follows the lines of *Macacus*, except that it takes in the ulnar edge of ring-finger, which I have never seen quite reached by it in Macaque. The VIIIth cervical area of HEAD in the hand represents with remarkable accuracy the central strip of the same field in *Macacus*, for it is a strip equidistant from the anterior and posterior borders of that field. Also the VIIIth field of *Macacus* has extensor and flexor peaks resembling those of HEAD's field. Between the fields of the Ist thoracic in man as determined by HEAD, and that experimentally delimited in *Macacus* the correspondence is again strikingly close, the latter being, as is inseparable from the difference of the two methods of determination, rather the more extensive; the determinations of the other clinicians for this root are not in good agreement with *Macacus*. In view of the above discussion as to whether the IInd thoracic nerve contributes to the muscles of the arm in Man as in *Macacus* the degree of correspondence between the skin-field of the root in the two cases is of special interest. Now, MACKENZIE's figure (a case of herpetic eruption, v. BÄRENSPUNG) displays a distribution of the root closely similar to that in *Macacus*, and HEAD's area, determined both by herpetic eruption and by reference in visceral disease, gives a still completer correspondence. Other clinical observers do not describe the IInd thoracic field. The correspondence between this field in Man, as described by HEAD and MACKENZIE, is so close as not to indicate that Man's plexus is more prefixed than Macaque's. It is true that one occasionally meets with sensory roots and motor roots varying independently as regards pre and post fixture; but that is not the rule. I cannot, therefore, help suspecting that our text-books on human anatomy may err in omitting the IInd thoracic nerve from the human brachial plexus, although I think the above observations prove a certain degree of prefixture in the prevailing type of human brachial plexus as compared with Macaque's—in this point resembling the Cat's plexus—as compared with *Macacus*, Rabbit, Dog, and Rat. The fact that in *Macacus* the Ist thoracic does not, as it does in Man, send usually a branch to join the IInd thoracic, points in the direction of slight prefixture in Man, as does the muscular analysis. But HEAD's and MACKENZIE's observations of the area of the IInd thoracic in man seem to prove that the amount of his prefixture is after all small. It is certainly smaller in this region than in the lumbo-sacral, where, as I have shown in my previous papers, that both in regard to muscle and skin the human lies one whole segment in front of (*i.e.*, prefixed in comparison with) the Macaque type.

As just mentioned, the topography of certain skin-areas of painfulness and hyperalgesia, explicable by reference from visceral disease, has been investigated by HEAD, and shown by him to exhibit a segmental arrangement. This segmental scheme is, broadly taken, notably similar to that of the spinal root-fields as exhibited in *Macacus*. For instance, the areas of reference observe like the root-fields the great mid-dorsal and mid-ventral lines of the limb described above; a point of difference is that the former are individually less extensive and therefore exhibit less overlapping than the latter. The difficulty of minute comparison between the two is much enhanced by the frequent individual variation which I find obtain.

One noteworthy point issues clearly from their comparison, however. In the root-fields I met certain peculiarities of contour which recurred with such constancy that I soon came to recognise them as diagnostic for certain fields. These bold peaks and notches are obvious also in the visceral areas of HEAD, *e.g.*, the groin peak from the XIIth thoracic, the lateral flap upwards from the Vth thoracic, the lateral flap downwards from the IIIrd cervical, the axillary peak of the IInd thoracic. The similarity is too significant for chance coincidence. Again, HEAD's weighty discovery that two fields of skin—an upper between IVth cervical and Ist thoracic, and a lower between Ist lumbar and Vth lumbar—are, as regards reference of visceral pains, virgin and blank, suffices of itself to establish the intimate connection of the two schemes. The situation of these gaps is, according to both sets of observations, the very region of most pure, of least complicated, limb character. *Exact* and *absolute* correspondence between skin-fields of *Macacus* and Man is not to be expected, if, as I have, I think, proved above, the skin and muscles of Man are more prefixed than are those of *Macacus*.

SECTION II.—THE SEGMENTAL SCHEME OF INNERVATION IN THE LIMBS.

It was pointed out in my previous paper* on the innervation of the limbs, that there is, between the scheme of distribution of the motor and of the sensory spinal roots, a striking difference when the fields of the two roots are examined in the limbs, by on the one hand, motor nerves to muscles, on the other, sensory nerves to skin.

The motor root of each spinal nerve was found to supply a band of muscular tissue extending as a fairly continuous ray from the trunk and attached base of the limb laterally outward a greater or less distance toward the limb apex. The motor rays examined in serial order from before backward were found to extend further and further laterally, so that the hindmost two (or, in some individuals, three) reach and contribute to the extreme apex of the limb. Of the motor spinal roots supplying the limb each, even of those penetrating to the extreme apex of the limb, still contributes to the innervation of the muscles of the trunk. That is to say, none of the motor segments of the limb are detached from the median plane of the trunk. As instance, the 5th muscular ray of the pelvic limb, contributing as it does to the limb's extreme apex, nevertheless does not lose its base in the axial muscles of the trunk, but gives a share to such axial muscles as *sacro-coccygeus*.

With this arrangement of the motor roots the distribution of the sensory roots to the skin does not accord. The fields of distribution of the sensory roots as examined on the surface of the limbs are for those roots which supply the apex of the limb, widely disjoined from the median plane of the body, both dorsally and ventrally. The sensory arrangement is best described by imagining that into the proximal part of the limb on its dorsal and ventral surfaces the mid-dorsal and mid-ventral lines of the body have each thrust a spike, a secondary lateral axis, sidewise, almost at right angles to their own direction. Granted these side lines, the arrangement of the spinal skin-fields of the limb can be accurately stated by saying that they are ranged upon the secondary dorsal and ventral lines as though upon folded portions of the axial lines of the trunk itself. I gave further, in a previous paper,* reasons besides the above for believing the secondary axes to have a real, not merely hypothetical, existence.

Also, in another respect, the fields of distribution of the motor and sensory spinal roots respectively are, as examined in the muscles and in the skin of the limb, widely dissimilar. The motor rays segmentally composing the musculature of the limb are set in fore and aft series in such a way that the pelvic limb has a sloping anterior side,† because the rays entering the limb are, in front, four, of which each extends further into the limb than the immediately precedent ray. Along its posterior edge on the contrary the limb is composed in its whole length of one ray only, the VIth

* 'Phil. Trans.,' B, 1892, vol. 184.

† In other words, the anterior edge of the limb is not at right angles to the axis of the trunk, but encloses behind it with that axis an angle less than a right angle.

or most posterior of all those in the musculature of the limb. With the distribution of the sensory roots of the limb, as examined in the skin, the arrangement is different. The skin-fields of the sensory roots lie along the posterior face of the limb as well as along its anterior in an overlapping series, so that each member contributes to a sloping edge, and the middle member juts the farthest. It results, therefore, that the posterior as well as the anterior side of the limb is as regards skin sloping, and that neither side is covered by a single segment only.

When previously pointing out this discrepancy between the arrangement of the fields of distribution of the motor and sensory roots, I added* "it must be remembered that the fields of the sensory roots as delimited in the present research are cutaneous and literally skin-deep only. In such glimpses as we obtain of the distribution of sensory nerve-fibres to muscles they seem to correspond segmentally with the motor supply." "The difference between the arrangement found for the motor-roots and that for the sensory may really be due less to the comparison being of efferent with afferent distribution than to the comparison being of muscle with skin." I have now observations which, I think, prove the above suggestion to be correct. The observations are as follows :—

I. The phrenic, which may be taken as a muscular nerve, contains fibres from the IVth, Vth and VIth cervical spinal ganglia, *i.e.*, from the sensory roots of exactly the same spinal segments as those whence motor fibres are furnished to it.

II. Afferent fibres in the nerve to vastus medialis and femoralis muscles are traceable to the spinal ganglia of the Vth and IVth lumbar nerves of *Macacus*, that is, to exactly the nerves which furnish the motor innervation of those muscles. I showed previously that the afferent nerve-fibres of these muscles pass through the Vth lumbar root, but I failed to demonstrate them with certainty in the root of the IVth lumbar, although in this latter root the corresponding motor-fibres are easily detected. Returning to the experiments again, I have since found that by employing strychnia it is possible to distinctly detect the existence of afferent fibres from vastus medialis and femoralis in the root of the IVth lumbar, in addition to those in the Vth. The proof is furnished by the persistence of the knee-jerk under strychnia poisoning, after severance of the obturator and sciatic trunks and of all branches of the femoral nerve, except that to vastus medialis and femoralis, *together with section of the sensory root of the Vth lumbar nerve.* The jerk persists, although in a crippled manner; it is completely (with the reservation explained in next paragraph) abolished by subsequent section of the sensory root of the IVth lumbar nerve.

The same appears true for the Cat, if for Vth and IVth lumbar nerves VIth and Vth be substituted. But in the Cat I have twice observed a phenomenon, recorded by WESTPHAL, which might appear to invalidate the above evidence. WESTPHAL states, on the strength of two observations on the Dog, that after exhibition of strychnia the knee-jerk is obtainable after section of *all* the afferent roots of the

* 'Phil. Trans.,' B, vol. 184, *loc. cit.* I have since examined the sensory nerve-fibres in muscles, 'Journ. of Physiol.,' vol. 17, 1894.

plexus; these observations form a part of his evidence that the jerk is not a reflex. In spite of their importance I cannot find the observations to have been ever repeated by WESTPHAL or by others. Certainly, in the Cat, after section of all the afferent roots of the plexus, if strychnia be exhibited, a tap upon the patellar tendon occasionally evokes an extension of the knee, indistinguishable, as far as inspection can judge, from a true knee jerk. But the phenomenon is exceptional, not the rule; thus it occurred in two out of six experiments. The exceptional production of this condition by strychnia need not really confuse its regular effect of rendering sufficient for production of the jerk the comparatively slender afferent path in the IVth lumbar (*Macacus*) root, after section of which the jerk, even under strychnia, is as a rule absolutely lost.

III. In the case of the VIth post-thoracic nerve of *Macacus* and of the VIIth of the Cat, the discrepancy between sensory distribution, as examined in skin, and motor distribution, as examined in skeletal muscle, reaches its extremest degree; yet even there the sensory root supplies nerve-fibres to the same muscles which the motor root supplies.

Example.—M. sinicus: the motor and sensory roots, including the whole spinal ganglion of the right IIIrd, IVth, Vth, VIIth and VIIIth post-thoracic nerves excised; the motor and sensory roots of the VIth post-thoracic simply severed well proximal to the ganglion. Thirty-five days' interval allowed for degeneration; the animal then finally examined, and its nerves prepared.

The lumbo-sacral plexus proved, on dissection, to be of prefixed type.

On excitation of the motor root of the VIth nerve of the intact side, contraction was noted in the following muscles: tibialis anticus, extensor longus digitorum, peronei, tibialis posticus, flexor longus digitorum, gastrocnemius, extensor brevis digitorum, flexor brevis digitorum, semimembranosus, semitendinosus, biceps, pyriformis, muscles of the back abducting the root of the tail.

The following nerves of muscles were microtomed for detection of some fibres; in most cases they were examined by teasing also :—

Nerve-trunk.	*Number of sound myelinate fibres.*
n. to *tibialis anticus* and *extensor longus*	hardly any.
n. to *peroneus longus*	hardly any.
n. to *extensor brevis digitorum*	a few sound fibres.
n. to *tibialis posticus*	few, but more than to tibialis anticus.
n. to *flexor brevis min. digiti*	a fair number.
n. to *gastrocnemius*, mesial head	a large number of sound fibres.
,, ,, lateral ,, ...	a large number of sound fibres.
n. to *semimembranosus*	a few sound fibres.
n. to *semitendinosus*	a larger number of sound fibres.
n. to *biceps*	a great number.
n. *to all the hamstring group*—14 *bundles*	no bundle without sound fibres.
VIth post-thoracic nerve, including spinal ganglion and ventral and dorsal primary divisions of the nerve . .	the number of fibres in the ventral division must be more than half, and in the dorsal very nearly a half.
collateral cutaneous nerves of the toes—	
2nd toe, mesial side, dorsal twig	five fibres,
,, lateral side, dorsal twig	seventeen fibres.
,, ,, ,, ventral twig	about sixty fibres.
cleft between 3rd and 4th toes, dorsal twig	plenty.
,, ,, 4th and 4th toes, dorsal twig	at least a half are sound.
5th toe, lateral edge, dorsal twig	more than half are sound.
,, ,, ,, ventral twig	more than half are sound.

Example.—Cat: the motor and sensory roots of the Vth, VIth and VIIIth post-thoracic nerves excised, including the whole ganglion of each sensory root. The VIIth post-thoracic severed well on the spinal side of the ganglion. Time allowed for degeneration, forty-three days. The animal then finally examined, and the various nerves prepared. The lumbo-sacral plexus was found by dissection to be a moderate example of the prefixed class. The VIIth post-thoracic nerve contributed no twig to the obturator trunk. Excitation of the IXth post-thoracic root gave no contraction of the limb muscles.

The cutaneous distribution of the VIIth post-thoracic nerve in the Cat includes the foot both dorsal and plantar aspects, and the lateral aspect of the leg below the knee, reaching above the knee for a short distance only on the postero-lateral surface of the limb. On excitation of the motor root of this nerve on the side of the body in which it was intact, contractions were noted in the following muscles, tibialis anticus, peroneus, tibialis posticus, flexor longus digitorum, gastrocnemius, semimembranosus, semitendinosus, biceps, and in muscles of the back moving the root of the tail. Of the muscular ray thus innervated by the motor root of this nerve the distal part only is, therefore, covered by the skin innervated by the sensory root of the nerve. But, on examining the following muscular nerves for undegenerate fibres, the sensory distribution of the nerve was found to include the following muscles: *gastrocnemius*, both heads; *semimembranosus, semitendinosus, biceps, tibialis anticus, tibialis posticus*, and muscles of the back.

Nerve trunk.	*Condition of nerve fibres.*
n. to *sartorius*	no sound myelinate fibres.
obturator in pelvis	? a few minute myelinate fibres in the perineurium: none sound elsewhere.
obturator in thigh, deep division	no sound myelinate fibres.
,, ,, superficial division	no sound myelinate fibres.
n. to *tibialis anticus*	plenty of sound myelinate fibres.
n. to *extensor digitorum*	plenty of sound myelinate fibres.
n. to *tibialis posticus*	a number of sound myelinate fibres.
n. to *gastrocnemius*, lateral head, 5 bundles	87 sound fibres, 17 μ—2 μ.
,, ,, median head, 4 bundles	7 sound fibres, 12 μ—2 μ.
n. to *semimembranosus*, 3 bundles	94 sound fibres, 19 μ—2 μ.
n. to *semitendinosus*, 2 bundles	52 sound fibres, 19 μ—2 μ.
n. to *biceps*, 4 bundles	37 sound fibres.
the most lateral plantal digital	many sound myelinate fibres.
the most lateral dorsal digital	very few sound myelinate fibres.
the most medial dorsal digital	a fair number of sound myelinate fibres.
the Vth post-thoracic nerve-trunk from the scar outward for a centimetre	no ganglion cells or sound myelinate fibres, except a few minute ones in or near the sheath.
the VIth post-thoracic	condition same as that of Vth.
the VIIth post-thoracic nerve, with ganglion and ventral and dorsal roots and ventral and dorsal primary divisions of the nerve. The motor root	3 sound myelinate fibres, ? recurrent.
ganglion and abjoining piece of dorsal root	no degeneration, except where the scar is approached; there plenty, traumatic.
ventral primary division	great numbers of sound fibres.
dorsal primary division	about a half of the nerve consists of sound myelinate fibres.
the VIIIth post-thoracic nerve	condition as in Vth and VIth.

In the above evidence for the existence in the limb of complete sensory as well as complete motor rays, the most convincing item is perhaps that furnished by the primary dorsal divisions of the Vth, VIth and VIIth post-thoracic, and of the VIIIth cervical and Ist thoracic nerves of *Macacus*. I have previously* pointed out that these divisions differ from the similar divisions of all the other spinal nerves in not entering the skin; they are devoid of cutaneous branches. Their anomalous behaviour is confirmed by the examination of the cutaneous distribution of the nerve, which shows that these particular nerves have skin-fields confined to the limb proper (to the leg almost exclusively below the knee). They have, therefore, no cutaneous territory at all along the middle line of the body. But by the experimental method it is seen that after section of the motor roots of these particular nerves more than a half of the nerve-fibres in their primary dorsal divisions still remain intact; the intact fibres are sensory; the primary dorsal division, although not cutaneous, is therefore nevertheless largely sensory. When in the same way the contribution given by the sensory roots of these nerves to the muscular parts of the limb is taken into account, a ray of muscular and other tissue is found to extend between the sensory skin-cap supplied by the nerves of the apex of the limb only and the median plane of the body. The proximal portion of the sensory ray exists, but buried beneath the surface; this proximal part is therefore nowhere cutaneous, but is mainly muscular; the sensory ray in the muscular and non-cutaneous tissue stretches from its base in the muscles and ligaments of the vertebral column to an apex in the muscles and ligaments, &c., of the foot.

By the experiments cited this has been shown for the lower limb; it is also true for the upper limb and the VIIth and VIIIth cervical and Ist thoracic nerves. The dorsal primary divisions of these nerves, like those of the Vth, VIth and VIIth post-thoracic, do not possess cutaneous branches, thus differing from the primary dorsal divisions of all the other cervical and thoracic nerves.

Experiment. *M. rhesus.* The Vth, VIIth, VIIIth cervical, and the Ist, IInd and IIIrd thoracic nerves cut in the vertebral canal proximal to the root ganglia. Time allowed for degeneration 28 days. The primary dorsal divisions of the Ist thoracic and VIIIth and VIIth cervical nerves on excitation evoked no muscular contraction, but when teased and when examined in serial sections, a number of sound myelinate nerve-fibres were found in them; these must have arisen in the spinal ganglia. The muscular branches of the ulnar nerve contained a certain number of sound myelinate fibres (not so many as in instance quoted from the lower limb); so also the inner head of the median nerve, but neither of these trunks on faradic excitation evoked muscular contractions.

It has been shown above that the distribution of the sensory root-fibres in the last two cervical, and in the highest thoracic nerve, is, as regards skin, confined to the hand, forearm, and lowest part of the upper arm, nowhere approaching to the median line of the body. If we include the sensory fibres distributed to the deep parts, the distribution of these nerves does, however, come right up to the median plane, including the muscles and ligaments of the vertebral column. Thus in the upper

* 'Roy. Soc. Proc.,' 1892. 'Phil. Trans.,' B, vol. 184, *loc. cit.*

limb, as in the lower, the sensory ray when its nerves are examined by experimental degeneration, is proved to extend from the apex of the limb to the median plane of the body, in fact, to be a complete ray. The proximal part of the ray, however, just as in the pelvic limb, nowhere reaches the body surface, but lies beneath the surface, and is composed of muscles and deep tissues. If judged by skin alone it is wanting.

It becomes clear that absence of cutaneous branches from the dorsal primary divisions of the VIIth, VIIIth cervical, and Ist thoracic, and from the Vth, VIth and VIIth post-thoracic nerves proves to be simply a natural concomitant of their segmental position in the spinal series, and is a criterion indicating that they lie at the very centre of the limb regions, respectively brachial and pelvic.

IV. The spinal roots which are the source of the afferent nerve-fibres of the hamstring *muscles* can be determined by use of vaso-motor and of respiratory reflexes. The individual dorsal (posterior) roots through which the afferent nerve-fibres from a muscle pass, can be found by noting which are the roots whose section lessens or abolishes the reflex. In the case of the hamstring muscles of the Cat, I find these roots, subject to individual variation, are the VIIth, VIIIth and VIth post-thoracic; now the VIIth, VIIIth and VIth nerves are exactly those, the ventral (anterior) roots of which supply the innervation of the muscles in question. Further, the VIIth is the chief root of the muscles, both as regards sensory fibres and motor. It is noteworthy that the effects of excitation of these afferent nerve-fibres from muscle, both on blood pressure and respiration, were not the converse of, but similar in character, to those from internal saphenous nerve, though not so extreme.

The conclusion arrived at by each of the four lines of observation is, therefore, that the *afferent* nerve-fibres distributed in a given muscle arise in the *root-ganglia of exactly those spinal segments, whence emerge the motor-fibres for the same muscle.* In other words, the sensory nerve-cells, directly connected with a given skeletal muscle, are in any one individual always of the same segmental level as the motor nerve-cells connected with the same given muscle. The simplest reflex path connected with a muscle may, therefore, be expected to lie exactly in the particular segments whence issue the motor-fibres to the muscle. In the "knee-jerk" we have evidence of a muscular reflex arc, traceable usually principally *from* and *into vastus medialis* and adjacent part of *crureus*, and this affords, as it were, a test case for the above conclusions; it confirms them perfectly; it exemplifies them by its narrow local extent, and by the segmentally horizontal, correlative position of its motor and sensory components.

SECTION III.—THE SEGMENTAL ARCHITECTURE OF THE LIMB.

Owing to GOETHE and OKEN, the conception became established that the plan of architecture of vertebrate animals is that of a fore-and-aft series of structural units or segments fundamentally similar one to another. Successive morphologists have, since their time, made use of various tissues as indices in the study of the disposition of the individual component metameres. The recognition of the segmental arrangement had been originally due largely to the obvious character of the series of vertebræ and ribs. It was, consequently, the osseous parts that were chiefly appealed to in the earlier attempts at extending the segmental theory of composition of the body to the limb (CARUS, OWEN), and in endeavouring to recognise the individual segments in the limb. Osseous tissue, I would maintain, is really poorly suited to such a purpose. If the presence of five digits at the free end of the limb could be taken as indication that the number of segments in the limb is five, then might the osseous tissue be useful for the study. The criteria used in the observations in this paper are, I think, demonstrably preferable to those taken from the bony system, and they show that such a character as the number of digits is a useless one in the examination of the segmental theory. The wide employment of osseous tissue for the purpose may, perhaps, have been in part due to the abundance of palæontological data it could contribute, and it is for this reason the more to be regretted that—as I believe—the osseous system, in many parts, is quite unfitted to throw light on the existence or position of metameres.

GOODSIR early (1857) insisted that the nervous elements of the limb appear to indicate more clearly than the other of its constituents, the morphological construction of the part. None the less, the study of the segmentation continued to be pursued chiefly upon bones. Later, the musculature came in for a share of attention, and now the muscles of the limb seem to obtain a preponderant and, perhaps, undue amount of consideration in the matter. A difficulty in making use of the nerve-fibres lies, no doubt, in the existence of the complex limb-plexuses entangling the segmental nerves at their very outset, before they are even fully launched upon their distribution. This difficulty can partly be removed by careful dissection, although, as pointed out by W. KRAUSE,* dissection alone cannot adequately unravel the nerve-courses even in peripheral nerves. By using, however, the physiological laws of isolated conduction in nerve-fibres (MÜLLER), and of degeneration of nerve-cell processes (WALLER), the difficulties of the nerve-plexuses and nerve-inosculations can be completely set aside. This being done, the nerve-elements in the limb become the best guides available for the tracing of segmental architecture. That was the view of GOODSIR, and I share it for the following reasons. The nerve-cells are among the earliest cells in the body, to cease the exercise of reproductive activity, and especially is this true of the cells of the spinal ganglia and of the primary motor neurons of the spinal cord. Neither are these cells in any sense vagrant. Remaining from a very early period securely anchored in a spot of known metameric orientation, their cell-processes, *i.e.*, nerve-fibres, radiate out into the rest of the metamere, whose various elements they have to bring into relationship with themselves as central station. In fact, they follow up the extension of the metamere, not by the process in virtue of which the other tissue of the metamere extends—namely, by cell-division, but by individual growth and increase of the length of the already existing cell-branches. This power of comparatively unlimited increase in individual size by elongation of cell-processes,

* 'Beit. z. Neurol. d. oberen Extremität,' Leipzig, 1865; see Plate.

enables the nerve-elements, with less metamorphosis and less spatial displacement of its nutritional centre than occur in any other tissue, to meet the requirements of changed surroundings, in short, to become adapted with relatively slight transfiguration and dislocation. The pieces of the same individual cell can be traced, however far they may extend, by the physiological methods mentioned. A limitation to the use of the nerve-fibres as guides to the territorial extent of segments, though hardly to their indication of the broad position of segments is, however, placed by their habit—as it appears to be—of somewhat overstepping, in their ultimate growth, the actual limits of the parent metamere. This overstepping is not in the skeletal muscles and in the sensory structures of the skin greater than to include a half, or generally rather less, of the adjacent segment, and it is regular in figure and extent. It certainly does not seriously confuse the picture that it affords, of the general segmental plan of a part.

I have now to attempt an exposition of the general scheme of arrangement I believe evidenced by the facts detailed in the preceding sections. Before proceeding to such generalisation, it is well to obtain, however, some answer to the following questions:—Is the amount of overlapping of the skin-areas of the various spinal nerves equally great in all body-regions? Is the amount of overlapping of the various spinal nerves greater or less than that of the territories of peripheral nerve-trunks? Is the amount of overlapping of the distribution of the sensory spinal-roots in skin equalled by that of the distribution of the motor spinal roots in muscles? What functional significance can be attached to the overlapping?

Is the amount of overlapping of the skin-fields of adjacent dorsal (sensory) spinal roots equally great in all body regions? In my previous paper I stated that "I conclude that the anterior and posterior overlaps are extensive enough in the Monkey to provide that the skin taken along any line parallel with the plane of the segmentation is supplied by two adjacent posterior roots. It further seems certain that in some places the skin is supplied by three adjacent posterior roots." In instance of skin receiving a triple root supply, I mentioned a part of the planta of the Cat, and the nipple of the Monkey. To these I will add portions of the skin of the hand, where a triple over-lap is clearly demonstrable by the following experiment:—The VIIIth cervical dorsal (sensory) root of *Macacus* having been severed both on left and right sides in the vertebral canal, these are further severed on one side (*e.g.*, right) the dorsal (sensory) roots of the VIIth, VIth and Vth cervical nerves, on the opposite side (*e.g.*, left) the dorsal roots of the Ist, IInd and IIIrd thoracic nerves. The field of remaining æsthesia is then delimited in each hand. The lines of boundary will on the one hand be those of the posterior border of the VIIth cervical field, on the other hand, those of the anterior border of the Ist thoracic field. Now, as shown above, the field of the VIIIth cervical nerve includes every portion of the surface of the whole hand. Further, although a certain amount of asymmetry can be detected in some individuals in the root-distribution of right and left sides that is of great rarity in the lower extremity, and even more uncommon in the upper extremity, and is always quite small in extent. If, therefore, in a series of experiments of the kind under description the field of the VIIth cervical root is found to include in the left hand portions of skin included by the field of the Ist thoracic in the right hand, a triple over-lap of the fields of the VIIIth cervical, VIIth cervical, and Ist thoracic may be taken to be proven to exist there. And such is actually the case. The triangular area of skin on the dorsum and palm of the hand shown in figures between the two dotted lines marked 7 and 1, is an area of triple root supply. It is notable that the area increases in width as followed from the wrist to the fingers, including in the latter position the whole of the medius and the adjacent sides of index and annulus. The area lies along the dorsum and palm somewhat, but not much, towards the ulnar side of the mid-line of the hand.

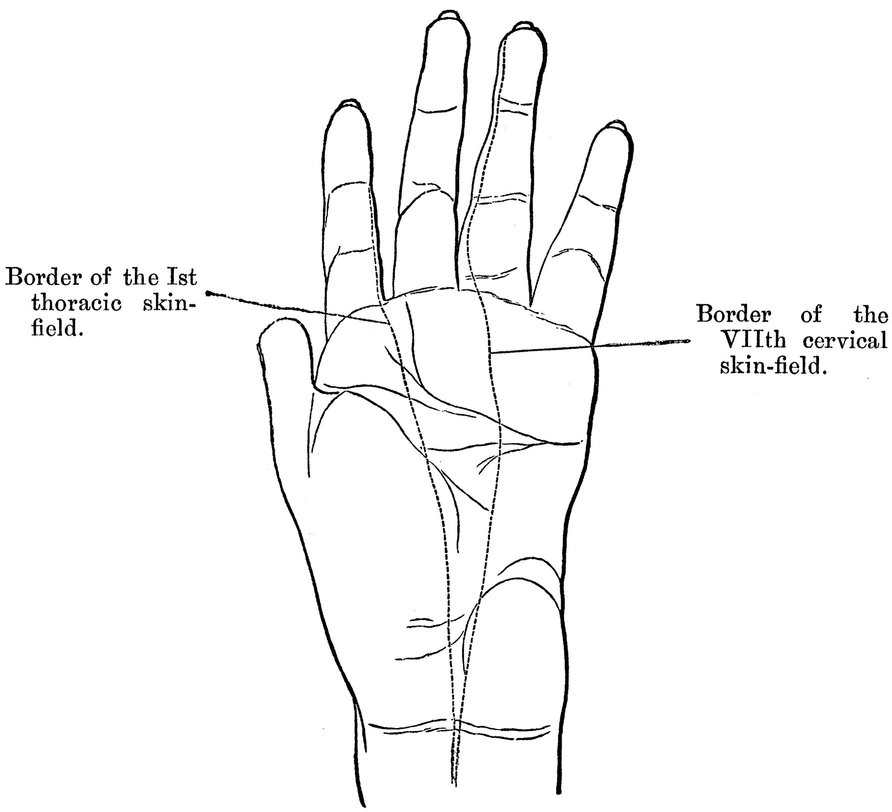
Again, the pinna of the ear is in part a region of triple overlap, namely in the fossa triangularis, tragus, opening of the meatus and part of the fossa of the anti-helix. In this latter portion it is probably a region of quadruple overlap, the curious little skin-field of the vagus, coming into combination with the fields of the cranial Vth, and of the IInd and IIIrd cervical nerves.

On the other hand, in certain regions, *e.g.*, along the back of the trunk about midway between the mid-dorsal and mid-lateral lines of the body, I think the amount of overlap of the root-fields in the skin of the Monkey is not so great as to amount to a full half of the contiguous field of each of the two consecutive nerve-roots. This point is, however, a difficult one to feel satisfied upon; experiments upon animals are really hardly suitable for deciding it; chiefly because in this region the degree of sensitiveness of the skin is comparatively low, and to obtain clear evidence of sensation, and therefore to have distinct knowledge of the extreme boundary of the field of remaining æsthesia is often by no means easy. The observations on which I rely, do nevertheless, distinctly indicate that in the dorsal region above mentioned, the amount of overlap of the consecutive skin-fields is less than, for instance, in the hand. It is, therefore, safe to say that amount of over-lapping of the fields of distribution of adjacent sensory spinal-roots is not equally great in all regions of the body.

Is the amount of overlapping of the fields of the spinal nerve-roots greater or less than that of the territories of peripheral nerve-trunks? That the skin-fields of neighbouring peripheral nerve-trunks do overlap is generally recognised, but very little experimental evidence exists on the subject. I have, therefore, made some observations on the foot and hand of *Macacus rhesus* and *sinicus*. I find the results much less open to individual variation than in the experiments upon the spinal nerve-roots innervating the same region. The figures illustrate the areas of anæsthesia obtained by section of the musculo-cutaneous and anterior tibial nerves, combined on the one side with section of the both plantar nerves, on the other with section of the external plantar only. It will be noted that the field of the internal saphenous nerve in the Monkey reaches along the tibial and dorsal aspect of the hallux very nearly to the tip of that digit. This is in agreement with the fact that, as shown in my previous paper, the Vth lumbar of *Macacus rhesus* has a skin-field which runs down upon that aspect of the hallux.

In *Macacus* the nerve seems to descend further along the hallux than it does in Man. It is true that in FLOWER'S 'Diagrams of the Nerves of the Human Body' (1881), the area of the internal saphenous nerve is given along the tibial aspect of the hallux, very nearly if not quite as far as terminal phalanx, and this although no overlapping at all is indicated. In THANE'S more careful figure of the cutaneous

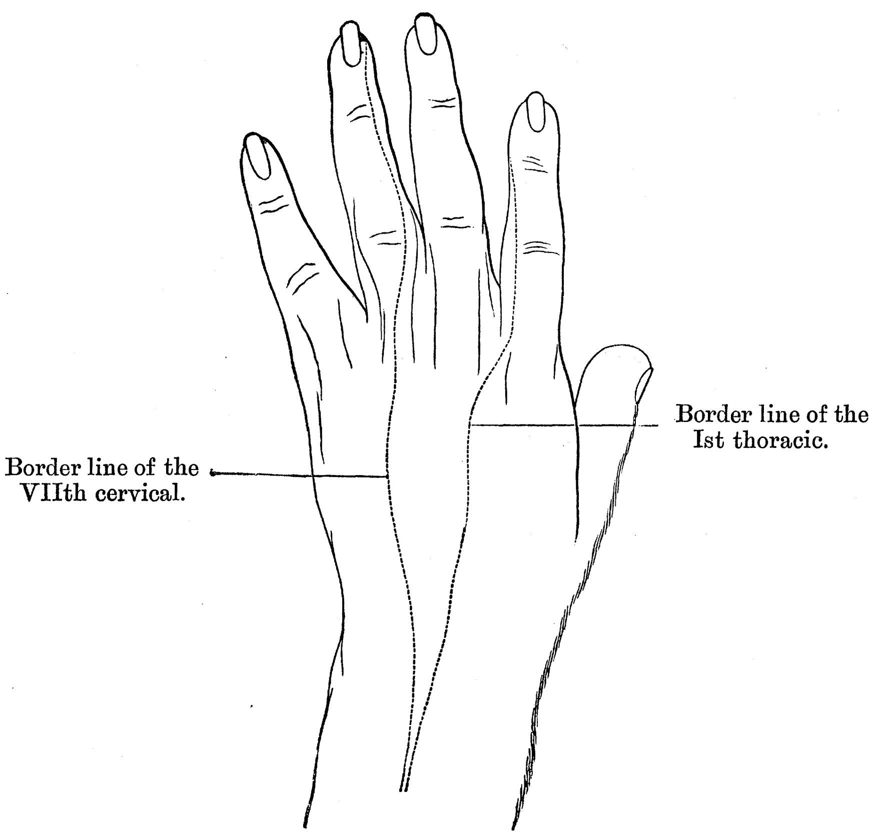
Fig. 7.



areas of the nerves of the lower limb (1895) in which overlapping is depicted, the area of the internal saphenous nerve is not carried so far down the hallux, and occupies part of its dorsal as well as of its lateral aspect. It is my belief that clinical observation can, on such subjects as this, afford more perfect information than can dissection. Through the kindness of Mr. R. JONES, of Liverpool, and Dr. CHALMERS, I have had the opportunity of delimiting the field of the internal saphenous nerve in a patient in whom a portion of the length of the sciatic nerve was excised high up underneath the gluteus maximus. I have been unable to find any previous instance of the clinical delimitation of the field of this nerve.

The patient was a well-grown young woman of German extraction, twenty-two years of age. Her answers, under examination, were particularly clear and intelligent. The condition noted at a period four weeks after the resection of the (right) sciatic was the following:—The border of the anæsthesia is delimited by a line which can be traced thus: Starting from a point just behind the head of the fibula, it crosses forwards and downwards below that point, and reaches the anterior surface of the limb lying upon the junction of the peroneal and pretibial groups of muscles. At the junction of the lower and middle thirds of the leg it sweeps forward, and at 1 inch above the level of the malleoli it lies to the tibial side of the median line of the limb. It then passes down about 1 inch in front of the internal malleolus, and thence to the top of the scaphoid. From there it turns back behind it to reach the inner border of the sole of the foot, at a point vertically below the internal malleolus, and afterwards

Fig. 8.



runs abruptly backwards along the internal border of the sole for two inches, toward the heel. About $1\frac{1}{4}$ inches in front of the point of the heel it again abruptly turns to pass upward between *tendo Achillis* and the internal malleolus, nearer the latter than the former. The line thence slopes across *tendo Achillis* obliquely to reach the fibular side of it, which it attains 2 inches above the level of the malleoli. It next slants across to the fibular side of the calf muscles, so that 8 centims. above the external malleolus it is placed only 3·5 centims. from the fibula and 5·5 behind the border already traced. It then runs nearly vertically over the calf muscles to the lower apex of the popliteal space, and continues to the top of that space (*i.e.*, to a point 10 centims. above the line of flexure behind the knee) in such a line as to fairly bisect the space. At 10 centims. above the line of flexure, it suddenly recurves so as to include an angle of not more than 35°, and descends in a slightly-curved line along the posterior border of biceps muscle: this it leaves at the level of the flexure of the knee, where it passes to reach the point from which the tracing of it was commenced. (See figs. 1, 2, 3, Plate 6.)

Measurements taken, were as follows:—

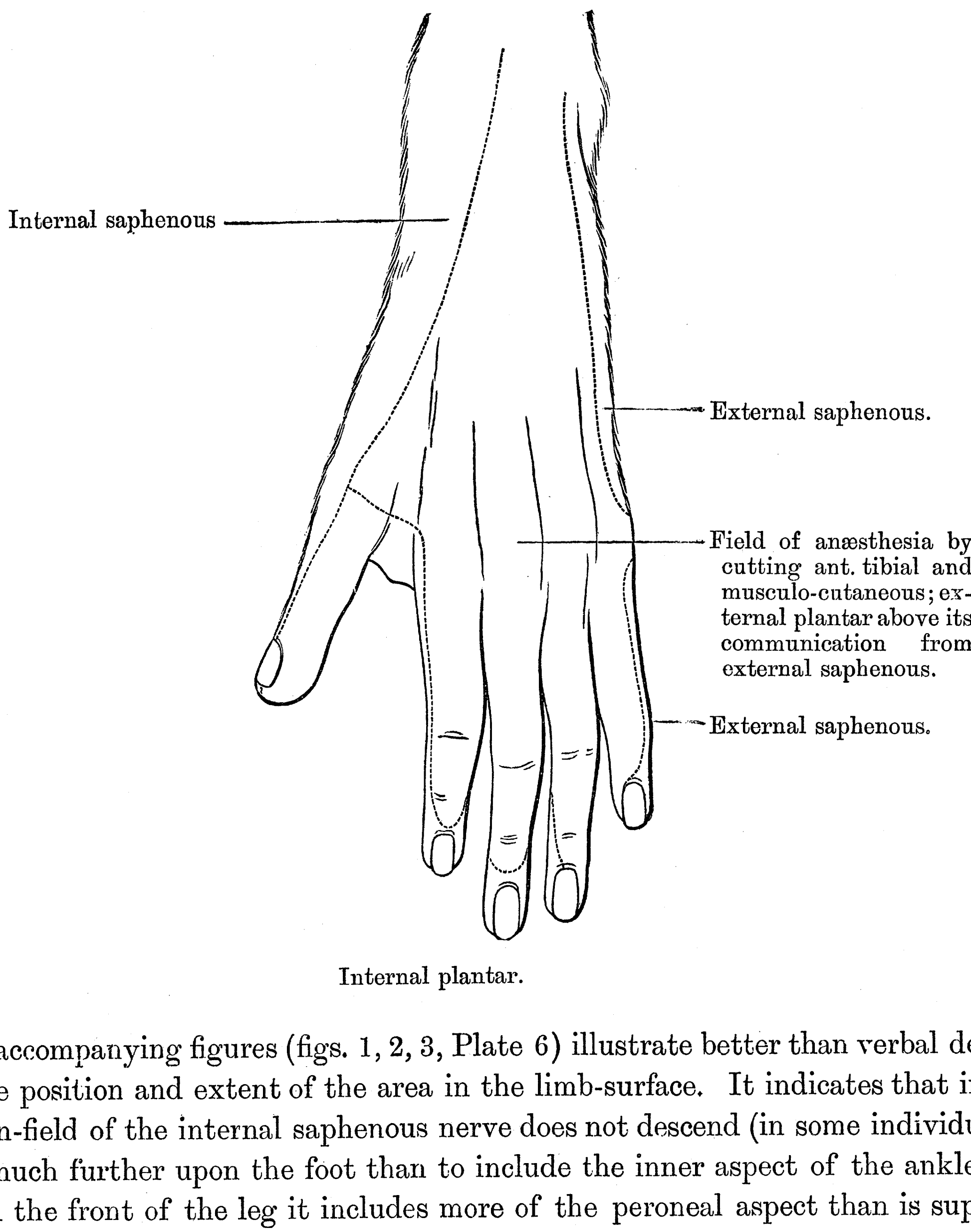
1. From head of fibula to outer malleolus measures 36 centims.

2. Narrowest width of the anæsthetic area lies at the level of the head of the fibula (width being 4 centims.).

3. At 1 centim. above the level of the tip of the internal malleolus, the width of the anæsthetic area measures 10·5 centims., the whole circumference of the limb there being 19 centims.

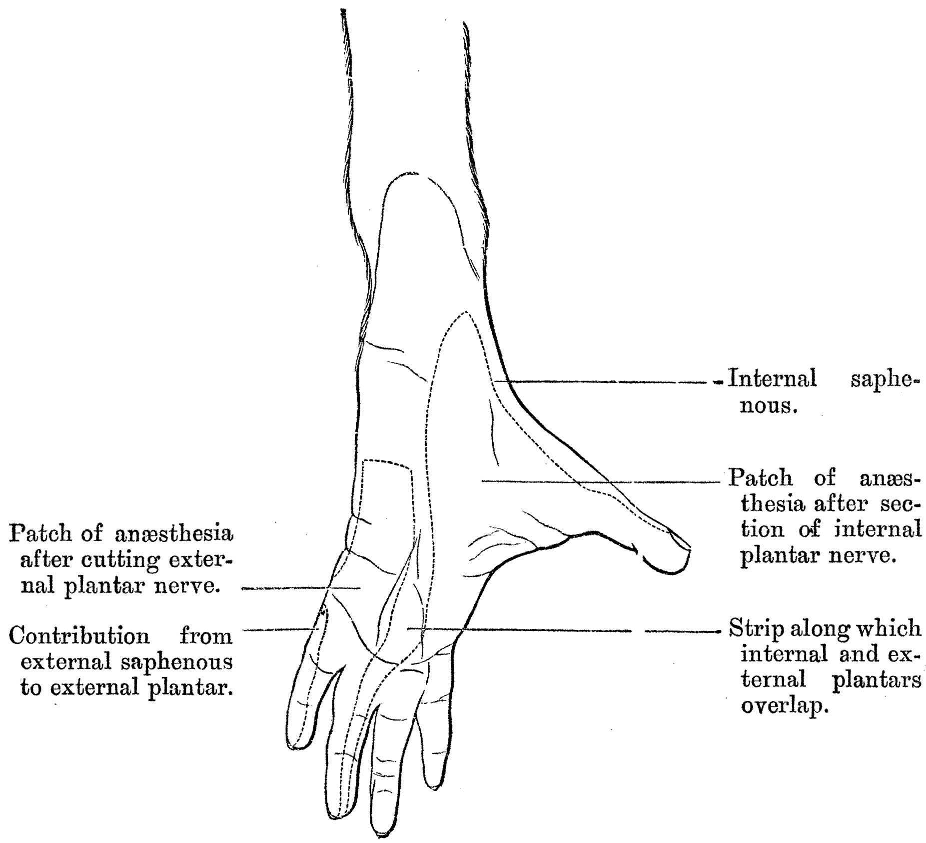
4. The internal malleolus lies just about equidistant from the anterior posterior and lowest edges of the field on the inner aspect of the ankle.

Fig. 9.



The accompanying figures (figs. 1, 2, 3, Plate 6) illustrate better than verbal description the position and extent of the area in the limb-surface. It indicates that in Man the skin-field of the internal saphenous nerve does not descend (in some individuals at least) much further upon the foot than to include the inner aspect of the ankle; also that on the front of the leg it includes more of the peroneal aspect than is supposed. It makes probable the greater wrapping round the thigh and knee of the cutaneous branches of the femoral and obturator-nerves; so that the internal cutaneous and obturator sweep from the inside back as far as the middle line of the ham, calf, and thigh, while on the outer side the external cutaneous innervates skin over the outer ham-string head of the fibula, and a portion of the outer head of the gastrocnemius and extends, perhaps, a fourth of the way from knee to ankle, instead of being confined to the thigh. This distribution in these directions, more extended than is usually supposed, favours the supposition that the overlapping of the skin-fields of the peripheral nerve-trunks is greater than is generally thought.

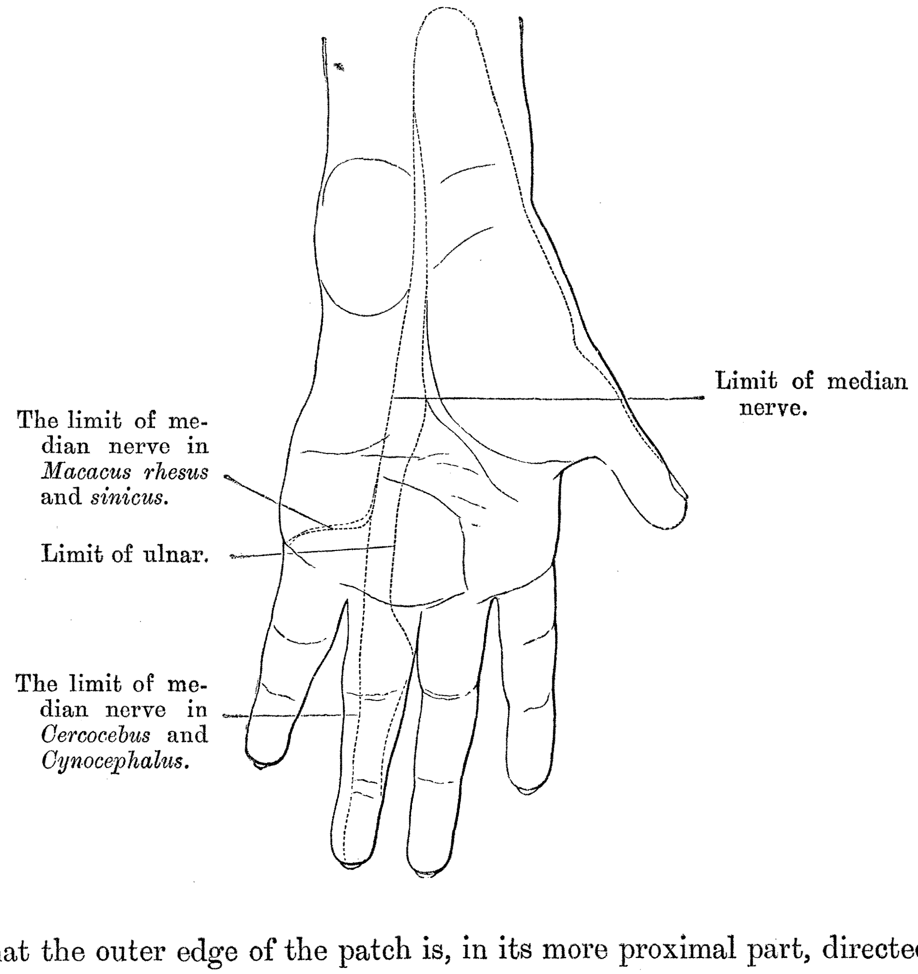
Fig. 10.



Returning to the skin-fields of the peripheral nerve-trunks supplying the Monkey's foot and hand, the above case indicates that the field of the internal saphenous is larger in the foot of the Monkey than in that of Man. Section of the musculo-cutaneous and anterior tibial nerves leaves the whole of the thumb, the plantar face, the sides, the nails and chief part of the dorsal aspect of the end phalanx of each of 2nd, 3rd, 4th, and 5th digits, and the outer third as well of the dorsum of the 5th digit still sensitive. Section of the external plantar being then performed, adds to the existing area of anæsthesia (1) the contiguous sides of the 4th and 5th digits,

(2) the corresponding lateral halves of their plantar aspects, (3) and of their terminal phalanges, dorsally as well, together with (4) an oblong strip of the outer part of the sole extending half-way to the heel. If, instead of section of the external plantar, the section be of the internal plantar, then the additional area of anæsthesia includes (1) the tip and all but a small dorsal strip of the rest of the hallux, (2) the tips, sides, and plantar surfaces of the 2nd and 3rd digits, (3) the tibial side of the whole length of the 4th digit, and (4) a triangular patch of the planta, including almost all the hairless part of the thenar eminence and inwards up to the middle line of the planta,

Fig. 11.

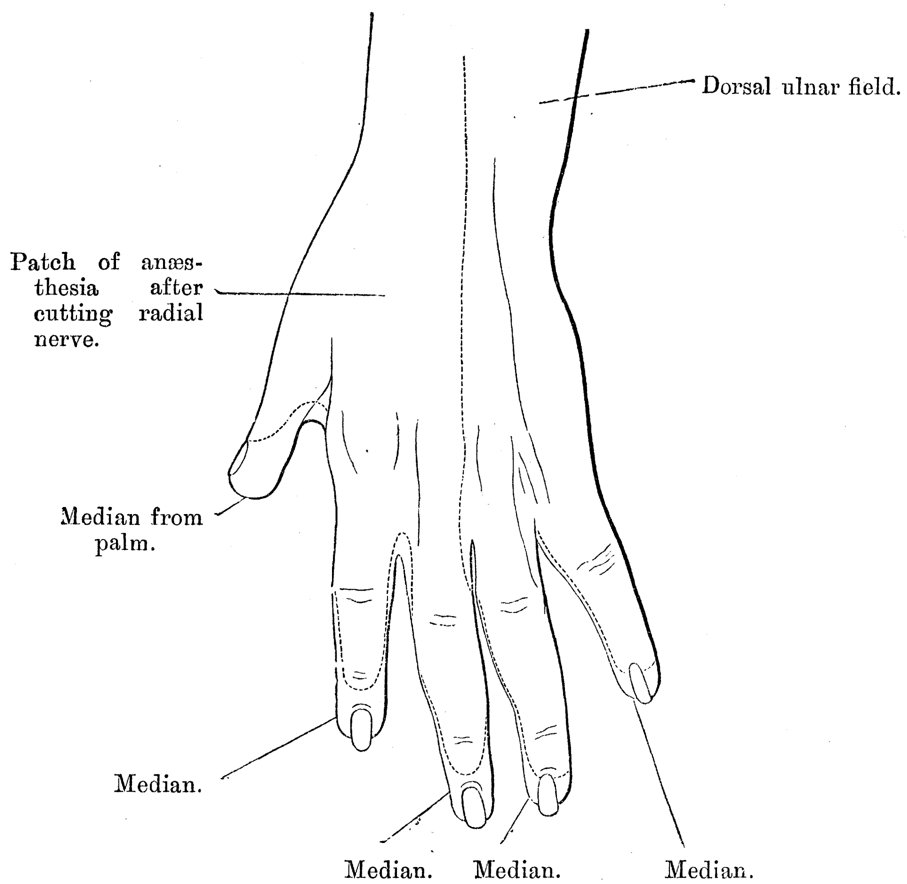


except that the outer edge of the patch is, in its more proximal part, directed toward the median line of the 3rd digit, and only over the distal end of the 3rd metatarsal bone curves outward to the outer side of the cleft between 3rd and 4th toes, to run along the plantar aspect of the 4th, distinctly on the tibial side of the middle line of that digit.

In my experiments, the field of æsthesia persisting upon the fibular edge of the foot and extending to the end of the 5th digit, has each time been distinctly separable into a smaller part on the digit, and a larger on the lateral edge of the metatarsus.

The distribution is more clearly understood by reference to the figures 9 (in text) and 10 than by verbal description. It must be remembered, in comparing them with Man, that, as I have pointed out,* there is a communication between external plantar and external saphenous of regular occurrence in *Macacus*, of which I find no record, even as an exceptional variety, in Man. The strip of overlap of the skin-fields of the external and internal plantar nerves is seen to be distinctly smaller than the overlap of skin between the VIth post-thoracic and the VIIth and Vth post-thoracic nerve-roots, indeed trifling as compared with that. In position it does not

Fig. 12.



lie in such a way as to suggest any commensuration at all between the two systems of overlap.

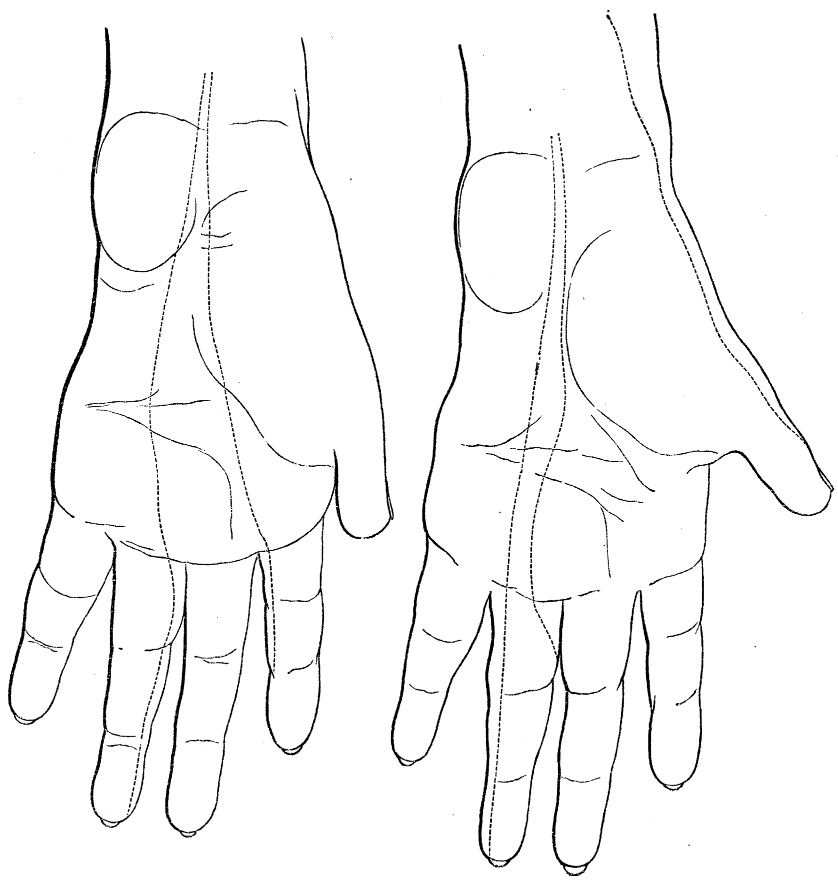
In the hand of *Macacus* the mutual overlap of the ulnar and median were examined after section of the musculo-cutaneous and musculo-spiral and internal

* 'Journ. of Physiol.,' vol. 13, 1892. It is not generally recognised that in the Monkey (*Macacus*), as I showed in my 'Lumbo-sacral Plexus,' the external saphenous nerve gives motor fibres to the short muscles of the foot, producing, when excited, interosseous flexion of all the digits.

cutaneous trunks in the upper arm. After the section of these nerves, the field of remaining æsthesia on the dorsum of the hand is that shown in fig. 12 by the dotted line along the middle of back of the hand and the dotted lines on the pollex and 2nd and 3rd digits. If the dorsal branch of the ulnar be then severed, the field of æsthesia is further reduced, and confined by the dotted lines on the annulus and minimus as on the three radial digits. On the palm, section of the median nerve in

Fig. 13.

1. 2.



Overlap of the skin-fields of median and ulnar nerve-trunks (1) compared with overlap of the skin-fields of the VIIth cervical and Ist thoracic segmental nerves (2).

the forearm produces a patch of anæsthesia, the limits of which are shown in fig. 11 by the line "ulnar." Section of the ulnar trunk halfway down the forearm produces a patch of anæsthesia with the limit marked by the line "median" in the figure.

In harmony with the difference of overlap of territories of the palmar nerves and of their spinal roots, is the much greater overlapping of the contiguous borders of the Vth cranial and IInd cervical than of the territories of the individual divisions of the Vth cranial itself (see above, p. 62), a difference which was made use of in determining whether those divisions were of segmental quality, or, like other peripheral nerves, functional rather than morphological entities.

It is then clear that in the hand, as in the foot of *Macacus*, the extent of overlap of the skin-fields of the peripheral nerve-trunks, even on the exquisitely sensitive plantar and palmar surfaces, is much less than that of the cutaneous areas of the nerve-roots; it is, in fact, not so great as may be the overlap of the fields of nerve-roots three segments distant one from another. If fig. 7, p. 102, be compared as in fig. 13 with fig. 11, p. 106, it will be seen that in the palm the region of triple overlap marked in the latter is greater than the medio-ulnar overlap in the former; and similarly in the fingers, if we set aside the communication between ulnar and median in the forearm, which is of only exceptional occurrence in Man. It is also notable that the region of triple overlap, which is the central region of double overlap, strikes a line on the palm which leads to and includes the medius digit, whereas the peripheral nerve-trunk overlap strikes a line leading to and taking in part of a different digit, namely, the annulus. This, again, points to there being no real correspondence between the two systems of overlap.

The answer arrived at to the question set is therefore that where examined an overlap of the skin-fields of adjacent peripheral nerve-trunks has been found, but that it is very small as compared with the overlapping of the skin-fields of adjacent nerve-roots and bears no significant topographical relation to the overlapping of the root-fields. On the other hand, I have shown previously* that the overlap of distribution of the constituent fibres of each nerve-root itself is even greater than that of the overlapping of contiguous nerve-roots.

Is the overlapping of the skin-fields of the spinal ganglia paralleled by overlapping of the muscular fields of the motor spinal roots? In the hind limb of *Macacus* I was able to confirm ECKHARDT's conclusions as to the pluri-segmental innervation of the limb-muscles, although ECKHARDT's observations had been confined to the hind limb of the frog. In the pelvic limb of *Macacus* I found but one muscle (tensor fasciæ femoris) with a nerve supply from a single spinal nerve-pair. The other muscles I found to possess a bi-segmental or tri-segmental nerve-supply; a fact since confirmed for the same limb in the case of Man by a research by PATERSON.† In the upper limb I find similarly that the muscles are pluri-segmental, a greater number being tri-segmental in the upper limb of *Macacus* than in the lower limb of that animal. The *subclavius* muscle seems in some individuals, as I found also *tensor fasciæ femoris* and *rectus capitis postici*, to be uni-segmental, receiving its motor supply sometimes from the VIth cervical nerve alone: it is in so far the only muscle I find uni-segmental in the upper limb. As examples of bi-segmental muscles, I find the teres major and anconeus. The palmaris longus, the supinator brevis, the supinator longus, anconeus, and the extensor carpi ulnaris may serve as types of tri-segmental muscles, and of quadri-segmental muscles the pronator quadratus, and flexor profundus digitorum (in

* 'Phil. Trans.,' B, vol. 184, *loc. cit.*

† 'Journ. of Anat. and Physiol.,' 1894, 1895.

some individuals). Muscles innervated from longer series still are the pectorales, and latissimus dorsi. On the other hand, in the intercostal spaces the intercostales externi and interni muscles appear, as far as I have yet examined them, to possess a strictly *uni-segmental* innervation, and somewhat similarly in the rectus abdominis, and in the sternalis these muscles have special zones for separate distribution of their motor roots. The multi-segmental nature of the nerve-supply, in the case of the large muscles at the attached base of the limb (pelvic and shoulder muscles), does not necessarily imply much actual overlapping or commingling of the muscular territories of the motor roots. I pointed out* that in the case of the lower limb there is much "greater overlapping and intermingling of the root districts in the muscles of the foot than in those of the thigh." The same is the case in the arm : the intricacy of the commingling in the muscles of the hand is much greater than in those of the shoulder. In the muscles of the forearm and hand the manner in which the nerve-fibres of a spinal root are scattered through the small muscle-nerves when examined by the degeneration method, gives a striking clue to the great commingling of the root territories in those organs.

To the question asked at the opening of this paragraph it may therefore be replied that there is in the musculature of the limbs, and of certain, though not all of the trunk-musculature, an overlapping of motor-root territories quite comparable with that of the cutaneous sensory root-fields; and the former, like the latter, attains at least as great a development as it attains anywhere in the distal ends of the limbs.

What functional significance may be assigned to the overlapping? Mindful that the overlap is maximal in the hand, and that of the structures under consideration here the hand may be considered supreme in sentiency of skin and nicety of action, it might be imagined that the pre-eminence of functional delicacy and of polymeric character of nerve-supply were determinate one of the other. That the two features may be correlated I should be the last to deny, but I fail to find proof of a causal nexus between them in the sense that one is result of the other. The overlap is as great in the skin of the back of the hand as it is in the palm, yet touch, as tested by localising power, is far the greater in the latter. It is medius not index which possesses the triple nerve-root supply, though medius is less sentient than index. The skin of the concha is not in *Macacus* apparently at all specially sentient, yet its sensory innervation is in part as regards nerve pairs a quadruple one. I am more inclined to connect the greater overlap in the hand and foot with degree of LOTZE's "local sign" and with the fact, indicated by the arrangement of the nerve-fields, that they lie approximately in the region of the lateral line of the animal as do the nipple and external auditory meatus, a line along which the amount of overlap seems to be great, perhaps as a heritage from old ancestral structure.

Examined by the degeneration method a somewhat greater degree of overlapping of root-distribution to the muscles of the limb is evidenced than examination by

* "Lumbo-sacral Plexus." 'Journ. of Physiol.,' vol. 13, 1892.

stimulation reveals. The degeneration method by its results explains the cause of the discrepancy between the observations by the two methods. The degeneration experiments show that in some muscles the number of motor nerve-fibres given by a spinal-root to a muscle is too small to evoke from the muscle any contraction at all obvious to inspection. Cases occur where a limb muscle receives one, two, three, four, or five motor-fibres from a particular root; allow to each of these motor nerve-fibres a dozen muscle-fibres, it is easy to understand that sixty muscle-fibres scattered in a muscle consisting of many thousands may cause no perceptible tightening of the tendon; they may simply stretch or compress adjoining inactive and elastic fibres. The degeneration of these few fibres I regard as strong evidence of the *morphological* character of the overlap; the fewness of the fibres is one of the many facts which indicate that the distribution of the motor-roots is arranged on a segmental plan in accordance with the terms of a bequest dating back to a time when the present environment of the limb, especially in its Mammalian form, had no preponderant weight in the shaping thereof. As regards functional value this character of the Mammalian limb is on a par with details of structure which are not specific, and, therefore, with other details of structure outside those immediately acquired by the species, not to be considered as of necessity of present functional importance. The functional use of the contribution of one or two nerve-fibres to a muscle requiring hundreds is difficult to see; the probability of the occurrence of such poverty-stricken contributions is, on the view of the morphological necessity of the ray-arrangement of the limb musculature, so high as to be only what might have been expected from theoretical considerations. The fact that certain of the motor-roots of the limb contribute fibres to the innervation of certain muscles in such scanty number as to be ineffective for movement is a further argument for the morphological rather than functional character of the motor-root distribution in the Mammalian limb. A number of motor-fibres, too small to evoke appreciable movement in a muscle when excited electrically, will hardly be effective for movement under the action of the will.

As to the relation between delicacy of co-ordination and number of nerve-roots contributing to motor innervation, one remembers that no muscles are more delicately adjustible than the ocular, although their individual innervation must be considered uni-segmental.

INDIVIDUAL VARIATION.

A point that is very necessary to bear in mind in the discussion of generalisations obtainable from the above data remains to be insisted on before entering on that discussion. In the innervation of muscles and of skin-surface in regard to the nerve-root which supplies the innervation, a certain degree of latitude of individual variation occurs with quite remarkable frequency.* In the fore-limb as in the

* SHERRINGTON, "The Lumbo-sacral Plexus." 'Journ. of Physiol.,' vol. 13, 1892.

hind-limb, this is the case, and examples have been mentioned in Section II. In the experimental basis of this paper instances have been particularly numerous with the VIIth and VIth cervical nerve; that may, however, be a fortuitous result. It would require a very large number of experiments to ascertain conclusively whether the peripheral distribution of those roots is more variable than that of the other brachial nerve-roots. I have already given evidence* that individual variation affects not one root alone but a series of consecutive roots; but it may, perhaps, reach its maximum at some one root of the series.

Since writing my previous paper I have met in the skin-fields of the lower limb a particularly pronounced example of individual variation in the distribution of the IInd lumbar nerve of *Macacus rhesus*. In two Rhesus Monkeys I severed the dorsal (sensory) roots of the IIIrd, IVth, Vth, VIth, VIIth, VIIIth and IXth post-thoracic nerves of the left side inside the vertebral canal. It is difficult in the region of the cauda equina to judge at the time of operation as to the exact segmental level of the nerve-roots exposed, and that has to remain, for the time being, a matter of doubt. When the operation wounds had well healed the field of remaining æsthesia was in each of the two Monkeys determined, not on one occasion only, but on many, indeed, almost daily for some weeks. In the one animal (A), the anæsthetic area did not extend up the front of the leg quite so high as to the patella, that is, the skin of the front of the thigh and over the patella (covering the patella) still retained sensation, distinct though impaired. In the other animal (B), the field of the anæsthesia extended fully two-thirds up the front of the thigh; sensation was retained in a tongue-shaped field of skin covering SCARPA's triangles, and lower down sensation was completely wanting. In (A) the skin between the anus and the tuberosity of the left ischium was anæsthetic, although between the anus and root of the tail, cutaneous sensation was distinctly present, though blunt. In (B) the skin lying between anus and left ischial tuber was for its half nearer to the anus distinctly sentient, as also above the anus between it and the root of the tail. From this, I did not hesitate to conclude that in animal (A) the IVth post-thoracic root, but not the IIIrd, had been included in the series severed, and that in (B) that IIIrd post-thoracic had been severed as well as the IVth, and I thought (B) in all probability an individual with a pelvic plexus of markedly postfixed type. I knew I had divided the same number of roots in the two individuals. The animals were kept after the operation wound was fully healed (10 days) for six weeks, and frequently compared; no obvious alteration in the extent of the anæsthesia was found to take place, although there were the usual small oscillations of briskness of reaction from day to day. The boundary remained stationary. On terminating the experiments and dissecting the two animals, it was found that in reality in both individuals the roots cut had been exactly the same. No spinal complication was

* SHERRINGTON, "The Lumbo-sacral Plexus." 'Journ. of Physiol.,' vol. 13, 1892.

detected to explain the difference, but in (A) the plexus was extremely prefixed, in (B), as I had expected, it was markedly postfixed.

In Monkey (A)—	Post-thoracic roots.
External cutaneous nerve was formed from	IInd, IIIrd, IVth.
Anterior crural nerve was formed from	IIIrd, IVth, Vth.
Obturator nerve was formed from	IIIrd, IVth, Vth.

In Monkey (B)—	
External cutaneous nerve was from	IIIrd, IVth.
Anterior crural nerve was from	IVth, Vth.
Obturator nerve was from	IVth, Vth, VIth, the contribution from VIth being a very small slip.

The frequency and degree of this individual variation of root distribution must present serious difficulties in clinical determination of the segmental level of a spinal lesion; the *exact* seat of a spinal lesion will, because of individual variation, it seems to me, always baffle the clinician's knowledge so long as he has only the segmental level of skin points and muscles to serve as guides. I have not met in the brachial limb with any instance of individual variation so extreme in degree as the just-mentioned example from the lower limb. Slight degrees of variation appear to me about as common in the brachial as in the lumbo-sacral region. I also find them in the upper neck muscles. Does the individual variation affect the spinal root supply of muscles as much as it influences that of skin? In the case of the lower limb of Monkey and Cat I have already pointed out that it does do so; and the observations on the upper limb confirm the information obtained from the lower to the same effect. One and the same muscle, just as one and the same skin-point, is in many individuals, distinctly differently innervated as regards relation to spinal segments, from its segmental innervation in other individuals. For example, the extensor carpi radialis brevior receives in some specimens of *Macacus rhesus* motor nerve-fibres from the Vth cervical root, in many specimens, on the contrary, it does not. The extensor longus pollicis in some individuals receives motor fibres from the VIth cervical root, in many it does not. The extensor carpi radialis brevior in some individuals receives fibres from the VIIIth cervical root, in many it does not. And so on.

Before leaving this subject I will add that one meets certain instances of bilateral asymmetry of segmental innervation. Occasionally I have seen the extreme form of postfixed lumbo-sacral plexus of *Macacus*, in which the IXth post-thoracic root innervates the muscles of the foot, occur on one side of an individual and not upon the other, although usually, of course, bilateral. In the Cat I have altogether met with five individuals in which the IInd thoracic root contributed to the innervation of the palmar muscles upon one side and not upon the other; and it is noteworthy that the postfixed side was in some left, in some right.

In the light of the observations recorded here it is instructive to compare the general scheme of root distribution in the arm with that in the leg. As in the latter,* so in the former, the cutaneous spinal fields become distorted from the simple zonal figure obtaining in neck and trunk. In the limbs they are displaced, and in the forelimb in a manner similar to that obtaining in the pelvic limb. In each limb the cutaneous spinal segments are dislocated. Instead of each being by one of its borders attached to the mid-dorsal line of the body, and by one of its borders to the mid-ventral line of the body, the fields are ranged along certain dorsal and ventral lines in the limb surface. It is as though into the base of the dorsal surface of the limb the mid-dorsal line of the body thrust a spike sidewise, a lateral branch, set in a direction almost at right angles to the long axis of the body itself, but corresponding with the long axis of the limb. On the ventral surface similarly the mid-ventral line of the body thrusts out a lateral branch. These lateral branches are what I have termed the *mid-dorsal* and *mid-ventral lines of the limb.* I have brought forward evidence to prove that they are not merely hypothetical, nor even merely theoretical, but are existent, and govern skin-markings† to a certain extent. On these secondary dorsal and ventral lines the skin segments of the limb are ranged as though on folded pieces of the axial line of the trunk itself.

The Mid-ventral Line of the Upper Limb. (Plate 5, figs. 19, 20, and fig. 4 in text, p. 66.)

This line starts from the mid-ventral line of the body, at a point on the sternum opposite the lower border of the 3rd costal cartilage. It passes laterally outward and a little upward on the pectoral mass, passing about two fingers-breadths above the nipple, *i.e.*, somewhat lower than midway between nipple and clavicle; it sweeps out to the upper arm below the anterior edge of the deltoid, and runs down the prominence caused by the mass of the flexors of elbow. On that prominence it keeps near the inner edge of the biceps; it enters the forearm upon the tendon of the biceps, and may be considered to terminate in the upper third of the forearm, at a point on the flexor aspect somewhat nearer the radial than the ulnar border. The fields arising from it in front are the IVth, Vth, VIth and VIIth cervical, and, in part, the VIIIth cervical. The fields arising from it behind are the IIIrd, IInd, and Ist thoracic, and, in part, the VIIIth cervical. The line, when the arm is out straight, runs about at right angles with vertebral column. In nipple line it lies just above 3rd costal cartilage, in the mid-lateral line it also lies over 2nd intercostal space.

The Mid-dorsal Line of the Upper Limb. (Plate 5, figs. 18, 21, and fig. 5 in text, p. 67.)

The dorsal line of the upper limb starts from the mid-dorsal line of the trunk, at a point opposite the root of the spinous process of the scapula, and just below the level of the head of the 4th rib. It passes laterally, and reaches the vertebral border of

* Phil. Trans., B, vol. 184, 1892, *loc. cit.*

† *Ibid.*

the scapula at the root of the spinous process; thence it slopes downward, crossing the infraspinous fossa just about midway between the scapular spine and the inferior angle of the scapula, and meets the posterior border of the deltoid eminence, but follows that only so far as to gain the eminence caused by the triceps muscle; along the middle of the crest of this eminence it runs to the elbow, and it enters the forearm between the olecranon and the outer condyle close to the latter. It terminates in the upper half of the forearm, on the extensor aspect behind the prominence of the radial extensors of the wrist, but somewhat nearer the radial than the ulnar border.

The spinal nerve-fields arising from it in front are the IVth, Vth, VIth, VIIth, and, in part, the VIIIth cervical, and from it behind arise the IIIrd, IInd and Ist thoracic, and, in part, the VIIIth cervical.

These great ventral and dorsal lines lie presumably along the centres of the primitive or true ventral and dorsal surfaces of the limb. As regards the primitive position of the forearm and hand, it is shown by the skin-fields of the spinal nerves to be that of supination. The skin of the pollex is shown to be segmentally anterior to that of the middle finger, that of the middle finger to that of the minimus. In the skin of the chest, just above the nipple, it is evident there is a meeting place of spinal nerve-fields, which, segmentally considered, lie wide apart; the IIIrd thoracic there meets the IVth cervical, or, in some individuals, the IVth thoracic there meets the Vth cervical. Where are the intervening nerve-fields to be sought? In part in the muscular tissue lying beneath the skin in this region; but as regards skin, they are to be found in the limb proper, and the midmost of the fields, *i.e.*, the VIIIth cervical, is placed almost entirely in the hand and forearm, that is, lies widely separated from the trunk, being confined to the apex of the limb. These lines of shed between anterior and posterior groups of skin-fields descend behind and in front of the shoulder along approximately the middle of the extensor and flexor aspects of the upper arm, and to a certain distance down the similar aspects of the forearm. In fore-limb, as in hind-limb, the skin of the anterior side of the limb is found to be segmentally rather more extensive than that of the posterior side, that is to say, those segments participate in it. In the musculature the preponderance of the segmental length of the anterior aspect over that of the posterior is still further marked.

As in the hind limb so in the fore limb, the quinquifid digital partition of the free end of the limb is (*contra* GOODSIR) no indication of the number of segments in the limb, or even in the free end of the limb, or even of the skin-fields or spinal nerve-fields in the free end of the limb. The number of spinal segments contributing to the limb is at least eight (apart from intrusions from the sympathetic); the number of segments in the free end of the limb, *i.e.*, hand is four; in the skin of the hand usually three, never five.

As remarked above, these dorsal and ventral lines of the skin of the limb are *not hypothetical.* In proof of this I have shown that the skin markings of certain animals—Tiger, Zebra, Ass, &c.—reveal them and stand in obvious relation to them. They have further considerable practical importance from the possibility that they, unlike other skin points, do not shift in segmental position with postfixture and prefixture of the flexures. As far as my observations on this point go, they indicate that these dorsal and ventral lines remain steadfast, although with postfixture and prefixture the skin-fields meeting at them are shifted.

In comparing the segmental structure of the brachial limb with that of the pelvic limb, certain points of resemblance are salient. One of these is the curiously similar distribution of the VIIIth cervical and the VIth lumbar nerves in the two limbs. Each of these nerve supplies in its respective limb the skin of the whole of the free apex of the limb (hand, foot), together with one surface of the more proximal part of the limb (forearm, leg). Each also supplies with motor and afferent fibres, a complete band of muscular tissue extending throughout the whole length of the limb from the attached base to the free apex. Of each the proximal part of the sensory distribution is buried in the deep tissues and nowhere reaches the cutaneous surface, whereas the distal part is distributed in the sensory nerves of the cutaneous as well as of the deep parts.

Striking, too, is the likeness existing between the distribution of the IInd thoracic nerve and the VIIIth post-thoracic nerve as regards the limb. Each of these nerves supplies the muscles at the apex of the limb (*e.g.*, the intrinsic muscles of hand and of foot). Each supplies also an analogous area of the skin, widely sundered from its muscular field, namely, an area of skin on the posterior face of the proximal portion of the limb (*i.e.*, the axillary extensor aspect of the upper arm as far down as a point close below the elbow; the skin over the flexor group of the thigh muscles to just below the knee).

To my mind, any attempt to trace out homologies between the brachial and pelvic limbs must pay regard to the remarkable resemblances between the contributions given by the above pairs of segmental nerves. For this reason I cannot subscribe to the antitropic scheme of homology recently revived by EISLER,* and worked out by him with such ingenuity and labour. In EISLER's scheme of homology the VIIIth cervical segment is the homologue of the IIIrd lumbar (of Man; the IVth post-thoracic of *Macacus*); the IInd thoracic segment is then made to correspond with the Ist lumbar (of Man). I cannot but insist that the analogy—and, in my opinion, nothing more than analogy has as yet been available, or at least employed, in instituting comparison between the limbs—between VIIIth cervical and Vth lumbar (of Man; VIth lumbar of *Macacus*), and between the IInd thoracic and the IInd sacral is infinitely greater than between any of the segments that are coupled together as homologous in EISLER's elaborate, careful, but to my mind untenable scheme of comparison.

My observations are, I consider, altogether adverse to any antitropic scheme; they

* 'Homologie der Extremitäten,' Halle, 1895.

are more compatible with a syntropia of the limbs. The composition of the anterior part of the brachial limb certainly resembles that of the anterior part of the pelvic limb more than it resembles the posterior part of that latter, in segmental structure both of muscles and skin. This greater resemblence is evident both in the number and step-like arrangement of segments and in the mutual relation obtaining in each segment between the position of its muscular and its cutaneous portions.

I must here, however, to avoid misapprehension, repeat my previously-expressed conviction, that it is altogether idle to look for exact homologies between the component parts of the brachial and pelvic limbs. "*The ontogeny of the brachial limb is distinct from that of the pelvic limb. The correspondence between the two is similarity, not identity. A general, but not a particular, resemblance is to be expected between the segmental components of the two,*"* and that is all that has been found. More instructive than to attempt to construe identity out of approximate resemblance is to note the fact that *broad similarity of requirement and use has from broadly similar segmental material evolved, at two places of the ventro-lateral aspect of the quadruped, two separate structures so curiously alike, as are the brachial and the pelvic limbs.* The details of this resemblance between the two appear to me absolutely insufficient criteria for establishing detailed homologies between their parts.

Anatomists teach† that in the higher vertebrata, at an early period of the embryonic existence of the limbs, a *rotation* of the limb, as a whole, takes place at its place of junction with the trunk. This rotation, at the proximal end of the limb, is described as occurring in opposite directions in the fore and hind limbs respectively. The fore-limb is rotated from the shoulder through nearly a quarter of a circle, so that the convexity of the elbow, which should point dorsally, comes to point backwards, and the edge, called by HUXLEY the post-axial (in reference to the axis of the limb itself), instead of being directed backward is directed inward towards the middle line of the body. The pre-axial edge of the fore-limb is conversely turned laterally outward. At the same time the hind limb is supposed to be rotated from the hip through 90° forwards ; the knee, thereafter, instead of presenting its convexity dorsally presents it toward the front, and the pre-axial border of the limb is, therefore, turned inward toward the ventral surface of the body, the post-axial edge laterally outward. The view of the position of the limbs of the Cat and Monkey, to which the observations in my own papers point does not correspond with the above. The analysis of the spinal nerve-root distribution, as insisted previously, shows the Monkey's limbs to be built up exactly on the plan of a lateral fin. The most definite pieces of surface to use as criteria to the topography of the limb are the mid-dorsal and mid-ventral lines above described. The pre-axial and post-axial borders of the limbs, which I have thought it clearer to speak of as anterior and posterior simply, are lost as borders where

* SHERRINGTON, "Lumbo-sacral Plexus." 'Journn. of Physiol.,' vol. 13, 1892.

† *Cf.* FLOWER and GADOW. 'Osteology of Mammalia,' p. 361, &c.

portions of the limbs become cylindrical, and this can be broadly said to have occurred in the upper arm, forearm, thigh, and leg of the Monkey; they never existed as borders in the attached bases of the limbs where the sessile limb-bud is fused with the trunk. It is, therefore, only in the hand and foot that these borders persist as borders, and there they meet, so that the point where posterior border ends and anterior begins can only be approximately decided. According to the received view, the pre-axial border contains in the fore-limb the outer condyle and greater tuberosity of the humerus, in the hind limb the inner condyle and the lesser trochanter of the femur. How far such deep-lying structures as two of the above can be parts of any "border" of the limb is not to me clear; be that as it may, the nerve-supply of the limb, as now analysed, shows that the above-named two points in the upper limb lie but little in front of the mid-dorsal line of the limb, and very greatly nearer to it than to the mid-ventral line of the limb, and can, for this reason, hardly be considered to lie in an anterior (pre-axial) surface of the limb, still less to constitute points in the pre-axial (anterior) border of the limb. Again, the two above-named points in the lower limb lie under the mid-ventral line of that limb, and are not parts of its pre-axial (anterior) surface, still less of its pre-axial (anterior) border. The point of the knee is by my evidence brought to belong to the anterior (pre-axial) surface of the limb, the point of the elbow to the posterior (post-axial) surface of the limb. The dorsal line of the limb, along arm and thigh, lie dorsally in the adult Cat and Monkey, and have not become displaced to any notable extent either backwards or forwards; the ventral lines in both limbs similarly lie ventral in the adult.

A *torsion* of the fore-limb about its own axis is traced by anatomists as having brought the distal end of the pre-axial border of that limb, during the pronate position of the fore-limb, into a position facing inwards. This view is borne out by the observations in my work. But the nerve-analysis in the Monkey indicates a slight torsion in the more proximal part of both limbs, for the distal end of the mid-dorsal line of the fore-limb is turned a little backwards as well as dorsally when, in a fore-limb capable like the Monkey's of supination at the wrist and elbow, the pollex is placed so as to correct the pronating torsion of the limb; and correspondingly the mid-ventral line passes on the flexor side of the inner condyle, that is, looks a little forwards as well as ventral. In the hind-limb the proximal part of the limb also exhibits a little torsion, and in the opposite direction to that evidenced in the fore-limb. The distal end of the mid-ventral line is set a little backward, that of the mid-dorsal line a little forwards. But in both the limbs the amount of torsion thus indicated is quite small, and the indication is of slight twisting, not of any rotation of the limb as a whole. The torsion accounts for the tongue-shaped extension from the posterior border of the successive spinal skin-fields in the brachial segments, shifting its position from—as followed along the limb—the point of the shoulder and the deltoid eminence to flexor aspect of the forearm, although assuredly the radial part of that. Conversely, in the lower limb the tongue from the hinder edge of the

Conspectus of Nerve-root Supply

	IInd Thoracic	Ist Thoracic	VIIIth Cervical
Back and trunk	Erector spinæ	Erector spinæ	Erector spinæ
	levator costæ	levator costæ	longus colli
	transverso-spinales	transverso-spinales	transverso-spinales
Shoulder	serratus posticus sup.	serratus posticus sup.	
	intercostales	intercostales	
	scaleni	scaleni	scaleni
			teres major
		pectoralis minor	pectoralis minor
		pectoralis major (lower edge only)	pectoralis major { sternal than
		latissimus dorsi	latissimus dorsi
Arm			coraco-brachialis
		triceps, (especially its inner head)	triceps
			anconeus
Forearm			extensor carpi rad. brevio
			pronator radii teres
		extensor indicis	extensor indicis
		extensor communis digitorum	extensor communis digito
		flexor carpi ulnaris	flexor carpi ulnaris
		flexor carpi radialis (very slight)	flexor carpi radialis
		extensor brevis pollicis	extensor longus pollicis
		extensor longus pollicis	extensor brevis pollicis
		extensor oss. met. pollicis	extensor metacarpi pollicis
		extensor carpi ulnaris	extensor carpi ulnaris
		extensor minimi digiti	extensor minimi digiti
	palmaris longus	palmaris longus	palmaris longus
	flexor longus pollicis	flexor longus pollicis	flexor longus pollicis
	pronator quadratus	pronator quadratus	pronator quadratus
	flexor sublimis digitorum	flexor sublimis digitorum	flexor sublimis digitorum

...UPPLY OF BRACHIAL MUSCLES IN A HIGH MAMMALIAN SPECIES (*Macacus*).

...Cervical	VIIth Cervical	VIth Cervical
	erector spinæ	Erector spinæ
	longus colli	longus colli
...s	transverso-spinales	transverso-spinales
		diaphragma
		rhomboidei
		subclavius
	serratus magnus	serratus magnus
	scaleni	scaleni (not always)
	deltoid (spinous portion)	deltoideus
	teres minor	teres minor
	teres major	teres major
	subscapularis	subscapularis
	supraspinatus	supraspinatus
	infraspinatus	infraspinatus
	pectoralis minor	
sternal part more than clavicular	pectoralis major { clavicular, sternal }	pectoralis major { clavicular, sternal }
	latissimus dorsi	latissimus dorsi
	biceps (slight)	biceps
	brachialis anticus (slight)	brachialis anticus
	coraco-brachialis	coraco-brachialis
	triceps	triceps (outer and long head)
	anconeus	
... brevior	extensor carpi rad. brevior	extensor carpi rad. brevior (slight)
...s	pronator radii teres	pronator radii teres (slight)
	extensor imdicis	
...s digitorum	extensor communis digitorum	extensor communis digitorum
...s	flexor carpi ulnaris (v. slight)	flexor carpi ulnaris
...is	flexor carpi radialis	flexor carpi radialis
...llicis	extensor longus pollicis	extensor longus pollicis
...llicis	extensor brevis pollicis	
...i pollicis	extensor metacarpi pollicis	extensor oss. metacarpi pollicis
...aris	extensor carpi ulnaris	
	extensor carpi rad. longior	extensor carpi rad. longior
...igiti	extensor minimi digiti	
	supinator brevis	supinator brevis
	supinator longus	supinator longus
	palmaris longus	
...cis	flexor longus pollicis	flexor longus pollicis (a few fibres)
...s	pronator quadratus	
...itorum	flexor sublimis digitorum (slight)	

Vth Cervical

Erector spinæ	Back and trunk
longus colli	Back and trunk
transverso-spinales	Back and trunk
diaphragma	Back and trunk
levator anguli scapulæ	Back and trunk
rhomboidei	Shoulder
subclavius	Shoulder
serratus magnus	Shoulder
scalenus medius	Shoulder
deltoideus	Shoulder
teres minor	Shoulder
subscapularis	Shoulder
supraspinatus	Shoulder
infraspinatus	Shoulder
pectoralis major (clavicular)	Shoulder
biceps	Arm
brachialis anticus	Arm
coraco-brachialis	Arm
extensor carpi rad. brevior (slight and occasional)	Forearm
extensor carpi rad. longior	Forearm
supinator brevis	Forearm
supinator longus (slightly)	Forearm

t)

)

	palmaris longus	palmaris longus	palmaris longus
	flexor longus pollicis	flexor longus pollicis	flexor longus pollicis
	pronator quadratus	pronator quadratus	pronator quadratus
	flexor sublimis digitorum	flexor sublimis digitorum	flexor sublimis digitorum
	flexor profundus digitorum	flexor profundus digitorum	flexor profundus digitorun
Hand		superficial short muscles of thumb	superficial short muscles o
Hand	deep short muscles of thumb	deep short muscles of thumb	deep short muscles of thur
Hand	lumbricales	lumbricales	lumbricales, 1, 2, 3
Hand	interossei: dorsal	interossei: dorsal	interossei: dorsal, all
Hand	interossei: palmar	interossei: palmar	interossei: palmar, 1, 2, 3
Hand	short muscles of little finger	short muscles of little finger	short muscles of little fing

	palmaris longus		flexor longus pollicis (a few fibres)
ɔis	flexor longus pollicis		
s	pronator quadratus		
itorum	flexor sublimis digitorum (slight)		
igitorum	flexor profundis digitorum		
uscles of thumb	superficial short thumb muscles	Hand	
; of thumb			
;	lumbricales, 1, 2		
all	interossei, 1, 2		
r, 1, 2, 3			
ttle finger			

——— nerve fibres d
.... nerve fibres d
——— contracts reg
～～～ contracts occa

)

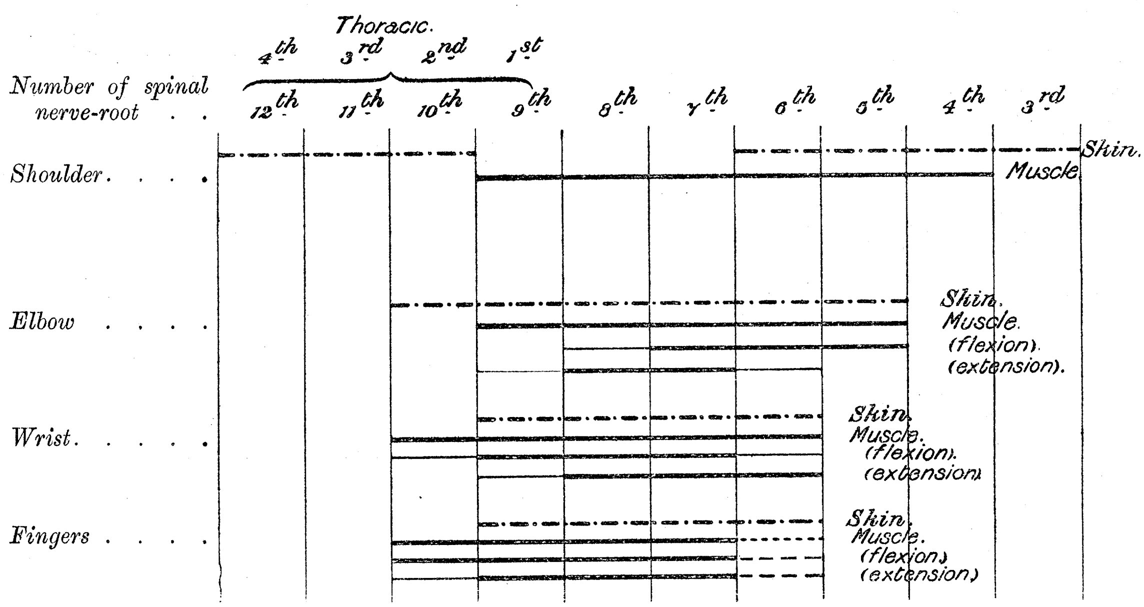
fibres degenerate regularly on section of root.
fibres degenerate occasionally on section.
acts regularly on stimulation of root.
ɪcts occasionally, *i.e.*, in some individuals.

spinal skin-field in the upper crural segments occupies the middle of the groin, and in lower segments gradually comes to lie over the subcutaneous surface of the tibia, and finally includes the hallux. But this torsion altogether is very slight.

The mode of distribution of the motor roots to the skeletal muscles (see accompanying "Conspectus") of the limb indicates that the limb is composed of a number of rays placed at right angles to the long 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 from the side of the trunk than is the posterior. Into the anterior edge enter a number of rays; taking six to be the number of muscular rays in the fore-limb of *Macacus*, into the segmental composition of its anterior edge there enter four out of the six.

If by a ray be meant a band of muscular tissue extending lengthwise through the musculature of the limb, it is not difficult by the degeneration method to trace in the limb the rays of the Vth, VIth, VIIth, VIIIth and IXth spinal segments, and to see that of these the last two extend out even to the extreme free end of the limb. The ray of the Xth segment is less easily traced throughout its extent continuously. The distal part of it is obvious enough in the intrinsic hand muscles; it is also clear in that part of it stretching between elbow and wrist, for there in *Macacus* it supplies the flexor muscles. But in *Macacus* it is unrepresented in the musculature of the upper arm, and in the Cat and Dog it is generally absent from the musculature of the forearm also. Indeed in the Cat it is often absent from the musculature of the hand itself. In Man it appears, as in the Cat, to be sometimes wanting altogether from the musculature of the limb, although not unfrequently it undoubtedly does contribute to it, then probably, as in the other types, occurring chiefly in the hand and flexors of the forearm. It is clear that, broadly described, the musculature of the fore-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 deltoid scapular group, including in that the clavicular part of pectoralis major. That the next step takes in the biceps and brachialis anticus and part of supinator longus, and the descent then follows down the radial side especially, until with the VIIIth cervical ray the whole length of the musculature of the limb is reached even to its extreme apex. The length of the limb thus having been attained, and occupied by successively longer and longer out-thrusts of four segments (just as I have described for the hind-limb), a number of other segments, usually two (Dog, *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 hand region that it is difficult to pick out from the rest any one muscle which shows more of this or that constituent. But in the forearm and arm it is less difficult; thus, in the former, the extensor communis digitorum receives a root which does not contribute to either of the long flexores digitorum, and the latter often receive a root which never contributes to the long extensor digitorum; in the arm triceps receives supply from two roots which never supply the biceps, the latter from one root which never supplies the triceps.

The details of the composition of the musculature of the fore-limb of *Macacus* by these six rays are given in the accompanying tabular statement. The fore-limb of the Monkey, just as its hind-limb, proves when examined by the analysis of spinal root distribution, to be a lateral fin with a sloping anterior and an abrupt posterior border, and this fin is built up of six rays.



Conspectus of segmental range of spinal innervation of the skin and muscles covering and moved by and moving the joints of the upper limb. The sensory innervation of the deep structures may be looked upon as similar (*see* p. 98 *supra*) in segmental range to the motor innervation of the muscles. (See text, pp. 122, 123.)

With regard to HERRINGHAM's generalizations* regarding the scheme of innervation of the musculature of the limb, my observations are in complete harmony with his rule, that: "Of two muscles, or of two parts of a muscle, that nearer the head end of the body tends to be supplied by the higher, that nearer the tail end by the lower nerve." This is so: almost as a matter of course, if the limb, as the theory asserts, is built up of lateral extensions of the segmental series of the body. And if, as I urge, the members of this segmental series, when taken from before backward, jut further and further from the median plane of the trunk, there follows as a corollary from the first rule that second rule which HERRINGHAM lays down, namely, that the musculature of the apex of the limb belongs to segments posterior to some of those in the attached base of the limb. Here it is that the curious fact

* 'Proc. Roy. Soc.,' vol. 41, p. 441, 1887.

comes in—that the most posterior segment which contributes to the limb musculature contributes in each limb to the extreme apex and to the extreme base, but not to the upper arm (or thigh), so that the hindermost muscular ray is one with a break in its middle portion.

HERRINGHAM'S third rule runs: "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."

With this my results on the lower limb did not agree; and I look upon my observations on the upper as confirming in this particular those upon the lower extremity. HERRINGHAM'S conception of the musculature of the limb is, I take it, that of a central core derived from lower segments over-laid by a peripheral sheet derived from higher. The conception to which my own observations lead me is of a simpler kind—a series of fused, partially commingled, segmental muscular strata placed one upon another in such a way that, to transfix them in true antero-posterior series, one would in the upper arm enter the front of the deltoid and emerge at the inner head of the triceps, or in the forearm pass obliquely from the extensors of the wrist near the radial border and out through the flexors near their ulnar border. The muscles on the extensor aspect of the wrist tend to be supplied by roots segmentally anterior to those which supply the muscles of the flexor aspect; and those near the radial border by roots segmentally anterior to those supplying muscles near the ulnar border. Hence the flexor profundus digitorum is segmentally posterior to the extensor communis digitorum, not because the former is deeper than the latter, but because the flexor aspect of the hand is posterior to the extensor aspect. I find the palmaris longus, superficial muscle as it is, and lying in the proximal region of the forearm as it does, is one of the most posterior muscles of the whole limb in segmental position; the flexor sublimis digitorum has in several observations seemed to me to contract more vigorously than the flexor profundus on excitation of the Ist thoracic, less vigorously than the flexor profundus on excitation of the VIIth cervical root. The fact that so deep-lying a muscle as the pronator quadratus gets the very posterior segmental nerve-supply recorded in my table, is probably explicable by its lying so distally in the forearm. A difficulty is, however, the superficial part of the intrinsic thumb muscles, which receives a, segmentally-considered, less posterior motor innervation than the deeper intrinsic thumb muscles. The anterior position of the thumb as compared with other digits may explain this, although the difficulty does appear to me considerable. In the leg, as I showed, the deep flexor of the toes is supplied by nerve-roots segmentally anterior to those supplying the soleus and gastrocnemius. The arrangement is not a different one in the two limbs; I believe it to be essentially the same; but it is more clearly expressed in the lower than in the upper; it was with the upper only that the work of HERRINGHAM dealt, and it is in that I admit that the arrangement which I consider to hold good, to the exclusion of the one formulated by HERRINGHAM, is the less clearly to be traced.

I have pointed out in a previous paper* that the spinal region of outflow of motor fibres is for the hip joint longer than for the knee-joint, for the knee-joint longer than for the ankle-joint. The segmental length of the region of outflow of motor fibres for a joint may be said, in the case of the hind limb, to be great in proportion as the joint lies proximal, less in proportion as the joint lies distal in the limb. Just as this rule is broadly true of the hind limb, so does it apply also to the fore-limb.† The outflow of motor fibres to the shoulder embraces six consecutive spinal nerve-roots, that to the elbow five, that to the wrist five, and that to the finger-joints four (if we omit the occasional supply from VIth to extensor metac. and flex. long. pollicis and the small contribution from the same root to the extensor digitorum). 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 is at least as long in the case of the distal joints of the limb as it is in the proximal, and the long region of motor outflow in the case of the large proximal joints is seen to be due—as I have already pointed out for the lower limb—to the motor representation of the main movements of each joint being more separated (*e.g.*, flexion more separated from extension) one from another in segmental position in the case of the proximal joints than in that of the distal. For example, for the movements of flexion and extension at elbow-joint flexion efferents leave the cord from the 5th, 6th, and 7th, and to a small extent also from the 8th segment, extension efferents on the other hand from the 7th, 8th, and 6th, and to a small extent from the 9th segment. The movements at the finger joints are on the contrary segmentally situated as follows: when judged by motor outflow from cord; flexion efferents from 10th, 9th, 8th, and to a less extent from 7th segments, extension efferents from 7th, 8th, 9th, and to a less extent from 10th segments, and still less from 6th segment. One might express the difference by saying that lengthwise along the cord the motor-nerve-cell groups for flexion and extension overlap each other very *slightly* in the case of the *proximal* joints, but very *largely* for the *distal* joints. In the case of the elbow, the extreme limits of overlap of flexion and extension motor-neuron groups embrace three spinal segments, but the overlap lies mainly in one segment, namely, VIIth cervical. In the case of the digits, the extreme limits of overlap of flexion and extension motor-nerve-cell groups embrace five spinal segments and lies mainly in two segments, the 8th and 9th. As result of this arrangement, antagonistic muscles are represented in one and the same root, most so when they lie at the distal end of the limb, less when they lie at the proximal end of the limb. Similarly, to the skin covering the hip a longer series of spinal roots contributes sensory fibres than contribute to the skin covering the knee, and still more so than contribute to the skin covering ankle and digits. In the upper limb, to the skin covering shoulder seven spinal ganglia contribute, to that covering elbow, six, to that covering wrist, four, to that covering fingers (excluding

* 'Journ. of Physiol.,' 1892, vol. 13, p. 748.

† See the 'Conspectus,' opposite p. 119.

thumb), three. Here, again, as a glance at the adjoining tabular statement shows, the long supply at shoulder is rendered still longer if we include the sensory ganglia supplying its *musculature,* for then the gap in the middle of its skin series is filled up, and we get sensory nerve-fibres for muscles and skin of shoulder-joint supplied by as many as ten spinal ganglia, from the IIIrd cervical to the IVth thoracic, inclusive. But if the muscular afferent nerve-fibres for the fingers are included, together with the digital cutaneous, the digital series is only increased from three segments up to four segments. Both distributions indicate the same general rule. The segmental representation in the motor spinal roots and in the spinal ganglia of the opposite movements and of the opposite surfaces of limb-joints is an overlapping one, and the overlap is greater for the distal joints of the limb than for the proximal. I look upon this arrangement as merely the physiological side of a morphological disposition, which latter has considerable ontogenetic significance.

Observations on the movements of the limb obtained in the Monkey by excitation of the separate individual cervico-brachial motor roots have been made first by FERRIER and YEO,* later by FORGUE and LANNEGRACE,† and by myself.‡ For the purpose of the present investigation I have extended my own experiments to the upper cervical roots which the above-named workers did not include in their investigations. My results are given in the subjoined table :—

Ist Cervical Root.—No movement of limb proper. Lateral adduction-flexion of the neck toward the side stimulated without rotation of the head.

IInd Cervical Root.—No movement of the limb proper. Lateral adduction-flexion of the neck toward the side stimulated, with some retraction. Little or no rotation of the head, but the chin may be turned slightly toward opposite axilla.

IIIrd Cervical Root.—No movement of the limb proper. Lateral adduction-flexion of the neck toward the side stimulated with marked retraction and a little turning of the neck, so that chin is thrust upward toward opposite side.

IVth Cervical Root.—Elevation of shoulder dragging it headward and toward the spinal column. Slight lateral adduction-flexion toward side stimulated with marked retraction. When the shoulder is fixed the slight turning of the head toward the opposite side previously obtainable becomes more pronounced.

Vth Cervical Root.—Elevation, abduction and some outward rotation of the shoulder; flexion of elbow, the wrist becoming slightly supine; slight radial abduction of wrist. Very slight lateral adduction-flexion of neck toward side stimulated, with some (slight) retraction of neck and head.

* 'Proc. Roy. Soc.,' 1881.

† 'Compt. Rendus,' 1884.

‡ 'Proceedings Physiol. Soc.,' Febr., 1892. 'Journ. of Physiol.,' xiii., 1892.

VIth Cervical Root.—Moderate adduction at shoulder; strong flexion of elbow; slight extension of digits and hand (not in every individual). Some supination of wrist, slight extension of wrist in most individuals, but in a few flexion and not extension of wrist. In one individual flexion of fingers was obtained from this root, but that may have been due to mechanical effect of extension of wrist, which if extreme in *Macacus* partially flexes the fingers. Very slight lateral adduction-flexion of neck toward side stimulated and slight retraction of neck and head.

VIIth Cervical Root.—Retraction and strong adduction at shoulder with some inward rotation of arm; the arm is carried across the body. Extension of elbow; slight flexion at wrist and some pronation; slight flexion of the fingers. The shoulder is drawn downwards. Slight retraction and lateral flexion of neck.

VIIIth Cervical Root.—The shoulder drawn downwards (latissimus dorsi). The adduction is not so extreme as in case of root VII. Rotation inwards of arm; flexion and pronation of wrist; flexion of fingers, and of thumb with opposition.

IXth = Ist thoracic.—Retraction of shoulder; slight lateral flexion and retraction of neck. Slight extension at elbow, flexion at wrist with pronation, flexion of fingers and thumb with opposition of the latter: there is usually a slight abduction of wrist toward ulnar side.

Xth = IInd thoracic.—Retraction of shoulder, slight flexion of wrist, flexion of fingers and thumb with opposition of the latter; sometimes slight pronation at wrist. Lateral curving of the spinal column.

My results agree, therefore, with those of FERRIER and YEO* more closely than with FORGUES and LANNEGRACE;† the latter omit the important IInd thoracic root altogether.

I subjoin some observations on the effect on limb movement of the section of certain roots, the rest remaining intact:—

Cynocephalus:—Total transverse division of spinal cord midway between the Vth and VIth cervical roots; the position was almost utmost flexion of both elbows, forearms three-quarter supine, fingers semiflexed, thumb slightly, and the elbows tilted rather forwards, the hands lying by their radial borders upon the mouth. The elbows could be voluntarily still further flexed, but not further unflexed. (Fig. 14 in text, p. 125.)

Macaque:—All the left side brachial roots, except the VIth cervical, severed in the vertebral canal and allowed to degenerate. The left upper limb was held constantly flexed at elbow at angle of about 100°; it was never extended, but was frequently still more fully flexed; the wrist was occasionally slightly extended; the arm could not be lifted voluntarily above the head; the fingers seemed quite paralysed; food was pushed into the mouth with the back of the wrist.

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* 'Proc. Roy. Soc.,' 1883.

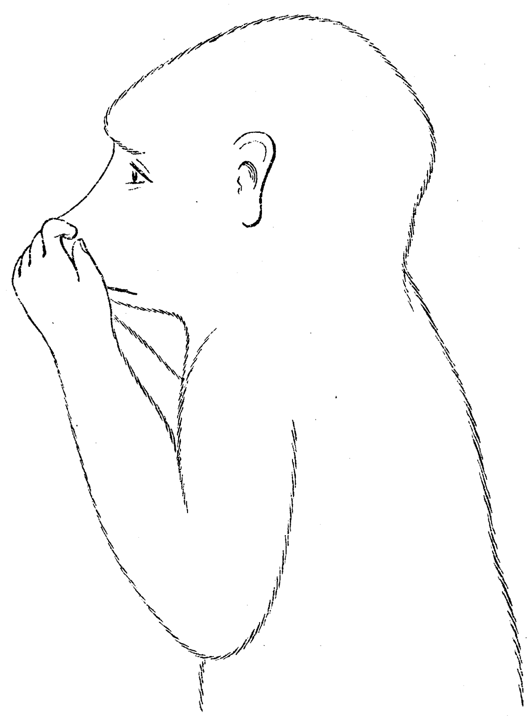
† 'Gazette Hebdomadaire des Sciences Médic. de Montpellier,' 1883.

Two Macaques :—The Vth as well as the VIth roots had been left intact, all the other brachial roots having been severed. The elbow was held flexed, the wrist was usually extended; the fingers were flexed at the metacarpo-phalangeal joints; supination of the wrist and active flexion of the fingers were movements sometimes seen.

Macaque :—All brachial roots severed except Vth, VIth and VIIth. The elbow was not held permanently flexed, but the fingers, except the thumb, were little used, although slight extension of the fingers was frequent as a willed movement.

Macaque :—All brachial roots except the VIIth severed. The elbow was kept permanently extended.

Fig. 14.



Macaque :—The Vth and VIIIth roots of the left side alone intact, the rest having been severed. Elbow and wrist and fingers could be flexed and extended; abduction of the wrist to the ulnar side was often noticed. The impairment of the limb was not very great!

Macaque :—The IInd thoracic root alone, of all brachial roots, left unsevered. The animal flexed its fingers voluntarily at times.

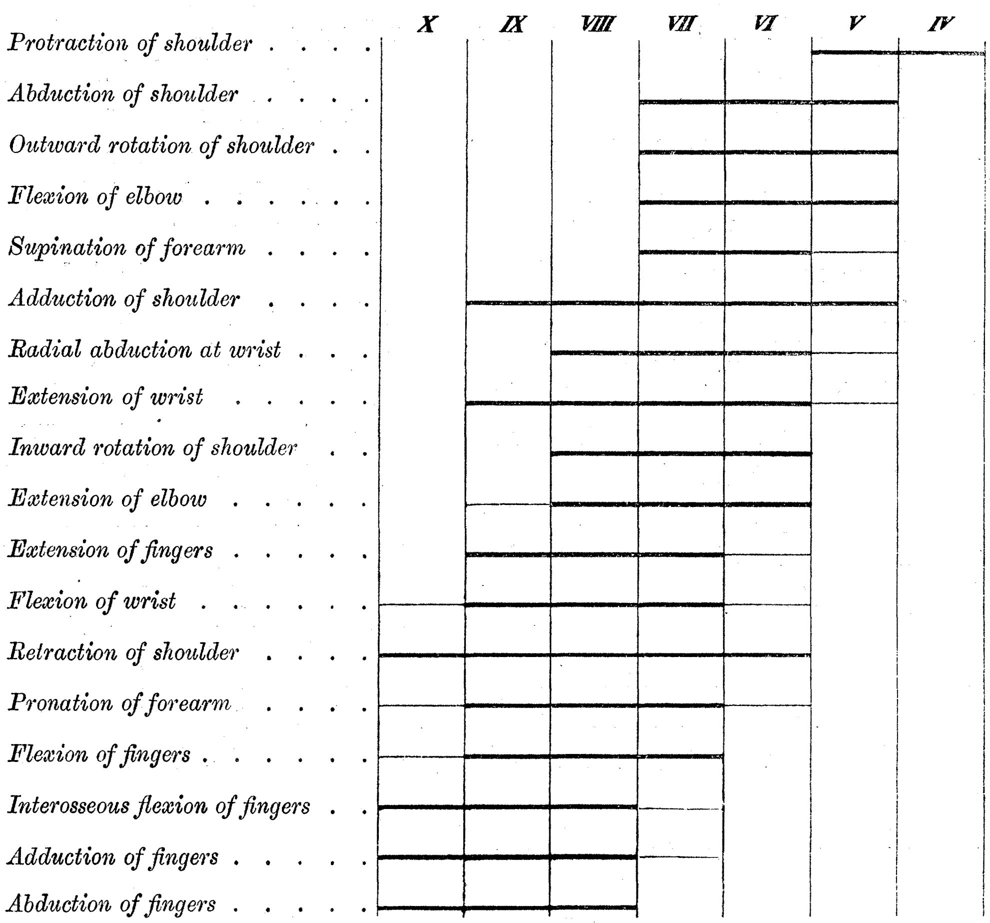
Monkeys in which the Vth, VIth, VIIIth and Ist roots were singly in different individuals severed and allowed to degenerate, displayed no obvious impairment of the movements of the limb, either immediately after the operation nor when the operation wound had healed.

From the foregoing, it is seen that by collating the combined movements obtained from each of the brachial series of roots, a *sketch* of the motor localisation of the limb movements is indicated; but the sketch is an *imperfect* one. As to the topographical order of the groups of motor nerve-cells executing the simple movements of the limb-joints, the analysis of the muscular fields of the motor roots carried out in my degeneration experiments yields a fuller and more accurate view of spinal localisation, considered in its fore-and-aft arrangement. The information from the combined movements evoked by nerve-roots is complicated by algebraic summation of component antagonistic factors, which as I have shown elsewhere is not of physiological value. Taken in longitudinal direction, the order of spinal localisation of simple limb movements in the brachial enlargement of the Ape is :—

protraction of shoulder.
abduction of shoulder.
outward rotation of shoulder.
flexion of elbow.
supination of forearm.
adduction of shoulder.
radial abduction of wrist.
extension of wrist.
inward rotation of shoulder.
extension and abduction of thumb.
extension of elbow.
extension of fingers.
flexion of wrist.
retraction of shoulder.
pronation of forearm.
flexion of fingers.
interosseous flexion of fingers.
adduction and abduction of fingers.
abduction of little finger.

So much mutual overlapping of the spinal representation of the simple limb-movements is present, that the above list does not give a very intelligible picture of the real topographical relationships of these motor centres. These are better represented in the following scheme :—

The scheme represents, by horizontal lines, the longitudinal localisation in the Ape's brachial spinal segments of the motor nerve-cell groups for the simpler functional muscle-groups of the limb.



Certain simple movements of the limb are not seen at all on the stimulation of individual motor roots: *e.g.*, in many monkeys no *root* gives extension of the pollex, and in some monkeys no root gives extension of the wrist, and I have met with an individual in which no root evoked extension of the fingers. In the Dog often no motor root dorsoflexes ankle or flexes the knee. In the Monkey, again, no root gives abduction of the pollex or little finger. If the muscles producing one movement at a certain joint predominate in one root, it does not follow those producing the opposite movement of the joint need predominate in another. Nor is the supposition borne out that muscles whose action predominates in one root always predominate in that root; thus, in the Cat, the VIth sub-thoracic root occasionally gives flexion of knee, though usually extension. In the Dog, the VIIth sub-thoracic root generally produces extension of the knee, and generally spreading of the toes, but occasionally flexion of knee, and occasionally flexion of the toes. The VIth cervical root of *Macacus* usually produces extension of the wrist, but sometimes flexion; the IInd thoracic of *Macacus* usually produces flexion of the wrist, but occasionally only flexion of the fingers and thumb.

The fibres in the motor roots of the brachial region are, as I have pointed out also for those of the lumbo-sacral region, from their very origin commingled in such a way that any one root-filament contains motor fibres for a variety of muscles, and often for muscles not concerned with the same simple movement of the limb. Commingled in this way at their source, they, after entering the nerves of the plexus, become sorted out into proper groups destined for particular muscles; hence the possibility of carrying out such dissections as those of HERRINGHAM* in spite of the difficulties on which W. KRAUSE† has so much insisted, and indeed stated to be insuperable. But within the motor roots themselves the fibres are so commingled that it is impossible, in one and the same root, to obtain, for instance, a bundle of fibres in one part of the root which represents flexion of the wrist, and a bundle in another part of the root which represents extension of the wrist.

It is clear that examination of the fore-limb does not, any more than did that of the hind-limb,‡ support W. KRAUSE'S§ statement that the skin at the free end of the limb is innervated by the nerve-fibres which, among fibres for the limb, are the ones most segmentally posterior; that opinion is clearly no longer tenable. KRAUSE, from his experiments and dissections on *Lepus* and *Cynomolgus*, also supported the "law" of VANDERKOLK|| and HILTON,¶ to wit, that a muscle is supplied with nerve-fibres by the same spinal nerve as innervates the skin overlying it. In this again KRAUSE is as directly controverted by examination of the fore-limb as of the hind. Also, in speaking of the longest nerve-fibres, as those in the VIIIth cervical root, KRAUSE must be ignorant of the fact that the Ist and IInd thoracic roots send nerve fibres to the intrinsic muscles of the hand.

SECTION IV.—SPINAL REFLEX ACTION.

The above examination of the peripheral distribution of the roots of the spinal nerves was undertaken "as a step preliminary to observations on the reflex functions of the spinal cord."**

Methods Employed.

For the purpose in view I found it essential to transect the cord; for the hind-limb region this was done sometimes at low levels, more usually above the Ist cervical root; almost exclusively at the latter situation in all experiments on the fore-limb region. In some experiments, as a control upon the spinal, transection was made at prepontine levels. It might have been thought that to examine spinal reflexes (*e.g.*, those confined to spinal paths) chemical narcosis would have sufficed, the longer

* 'Proceedings of the Royal Society,' vol. 41, p. 440, 1887.

† 'Beiträge zur Anatomie der oberen Extremität.' Leipzig u. Heidelberg, 1863.

‡ 'Phil. Trans.,' B, vol. 184, p. 641.

§ 'Beiträge zur Anatomie der oberen Extremität.' Leipzig u. Heidelberg, 1863.

|| FRORIEP'S 'Notizen,' 3rd series, 4, 129, 1847.

¶ 'Rest and Pain.' London, 1857.

** 'Phil. Trans.,' B, vol. 184, 1893. (Section IV. of this paper formed the matter of the Croonian Lecture before the Society, April, 1897.)

and encephalic paths being blocked earlier than the spinal. But as the experiments of MARSHALL HALL,* BERNSTEIN,† and CAYRADE‡ showed, the reflex activity of the isolated cord itself is soon depressed by anæsthetics; and an experiment in my former paper§ illustrated the ease with which chloroform lowers even the tonic activity of the spinal nerve-cells. My plan has been, therefore, after transection of the cord, to somewhat relax the general anæsthesia, and then to examine reflex action in the isolated portion of cord, all parts still connected with it having, of course, *ipso facto,* become insentient, *pace* the unproven *Rückenmarksseele.*|| In most cases the transection was made shortly prior to examination of the reflexes, but in some cases periods of recovery were allowed, extending at longest to six months. For excitation, mechanical, thermal, or faradic stimuli, usually approximately minimal, have been used.

In many cases it was noted whether the limb-plexus belonged to the prefixed or postfixed class. This it seemed necessary to do, as individual variation so frequently affects the relation between motor root and limb muscles (ECKHARD,¶ Frog; LANGLEY,** Cat; SHERRINGTON,†† Frog, Cat, and Monkey), and analogously disturbs the relation between skin and spinal ganglion (SHERRINGTON,‡‡ Frog, Cat, Monkey). The range of segmental oscillation can allow "in the origin of a root-filament a sufficient displacement to remove it from the upper to the lower half of the same root, or from the lower half of one root to the upper half of the next below," or conversely. Progress with the inquiry into reflexes showed, however, that two factors largely reduce the importance of individual particularities of distribution of the nerve-roots in regard to reflexes. One of these factors lies in the rule which I have already laid down that each root-filament, although its segmental level be displaced *absolutely,* yet is not displaced *relatively* to its neighbours, "the shift applying in the same sense to an extensive fore-and-aft series of filaments and those of the dorsal and ventral roots tending to be similarly affected."§§ The other factor lies in the rule of "spatial monotony," to be discussed later.

Reflex Movements Characteristic for the Individual Afferent Spinal Roots of Macacus.

The initial step of the inquiry has been to determine for the several dorsal spinal (afferent) roots the particular spinal paths easy of access through them. I have attempted to carry this out by noting the limb movement most easily provoked by

* 'Synopsis of the Diastaltic Nervous System.' London, 1850.

† SCHMIDT's 'Jahrbücher,' vol. 142, p. 227, and MOLESCHOTT's 'Untersuchungen,' 10, p. 280.

‡ 'Recherches sur les Mouvements Réflexes,' p. 48. Paris, 1863.

§ 'Journ. of Physiol.,' vol. 13, p. 671.

|| PFLÜGER, 'Die Sensorischen Functionen des Rückenmarks.' Berlin, 1853.

¶ 'Zeits. f. rat. Med.,' vol. 7, p. 306, 1849.

** 'Journ. of Physiol.,' vol. 12, p. 366, 1891.

†† 'Journ. of Physiol.,' vol. 13, p. 621, 1892.

‡‡ 'Phil. Trans.,' B, vol. 184, 1893.

§§ 'Journ. of Physiol.,' vol. 13, 1892.

excitation of the proximal end of each on the spinal side of the root-ganglion. In the regions of which I chiefly treat the vast majority of the afferent fibres are, in GASKELL'S sense, somatic. Besides, there is evidence that between somatic afferents and splanchnic efferents a high intra-spinal resistance exists.* I have, therefore, with few exceptions, disregarded sympathetic out-channels, believing the paths of least resistance, which were my object, would not lead greatly in their direction.

The movements obtained by excitation (minimal, or not far removed from minimal), of the spinal ends of dorsal (afferent) roots have been as follows (*Macacus*) :—

XIVth Post-thoracic Root.—Tail lifted and generally abducted, very often toward the opposite side; no movement of arms or of limb.

XIIIth Post-thoracic Root.—Tail lifted and generally abducted, very often toward opposite side; no movement of arms or of limb.

XIIth Post-thoracic Root.—Tail abducted, very often toward opposite side; no movement of arms or of limb.

XIth Post-thoracic Root.—Tail abducted, very often toward opposite side; no movement of arms or of limb.

Xth Post-thoracic Root.—Tail abducted, often to opposite side; protrusion of anus; no movement in the limb proper.

IXth Post-thoracic Root.—Tail abducted, less commonly to the opposite side; protrusion of anus; flexion of hallux, less frequently of other digits as well. It makes no difference to this movement whether the flexus be post-fixed or not.

VIIIth Post-thoracic Root.—Tail abducted to same side; protrusion of anus. The anal movement obtained from this and the two preceding roots is almost always protrusion, and rarely shows more than a trace of unilaterality, so that here again must occur a cross-path of low resistance athwart the median plane of the cord.

Flexion and adduction of hallux and flexion of other digits; slight flexion of knee (contraction of hamstring); slight plantar flexion of ankle (in one experiment this was bilateral, but more vigorous on the same side than on the crossed). When all the reflexes have been abolished by pushing the chloroform, the hallux reflex is usually the earliest to return.

VIIth Post-thoracic Root.—Tail abducted to same side; flexion of knee; flexion of hallux and digits, especially of hallux and 2nd toe; dorso-flexion of ankle (very rarely plantar flexion). When the filaments of this large root are separated into three sets, made up respectively of the anterior, middle, and posterior groups, no distinct difference between the replies obtained from each of the three is observable; crossed plantar flexion of ankle.

VIth Post-thoracic Root.—Tail abducted to same side; flexion of knee, flexion of

* SHERRINGTON, 'Journ. of Physiol.,' vol. 13, 1892, p. 732.

hip with some internal rotation; flexion of hallux and of other digits; less easily dorso-flexion of ankle with tilting up of the outer edge of the foot; adduction of thigh, easily obtainable as a crossed reflex.

Vth Post-thoracic Root.—Flexion of hip; flexion of knee (the inner hamstrings and the gracilis, perhaps, seem particularly active); flexion of hallux, loss of toes; slight dorso-flexion of ankle at times; adduction of hip as a crossed effect; movement of tail—not always.

IVth Post-thoracic Root.—Curving of body so that hind-limbs point toward side stimulated; flexion of hip; flexion of knee; flexion of hallux occasionally, and still less frequently accompanied by flexion of digits; quite rarely slight dorso-flexion of ankle; adduction of hip occasionally with crossed adduction.

IIIrd Post-thoracic Root.—Curving of body toward side stimulated, as above, but more so; flexion of hip, rarely flexion of knee; occasionally flexion of hallux and occasionally of other digits as well; drawing up of cremaster.

IInd Post-thoracic Root.—Curving of body, as above; flexion of hip; drawing up of cremaster; very occasionally flexion of hallux.

Ist Post-thoracic Root.—Muscles of flank contract; some retraction of abdominal wall low down; flexion of hip.

XIIth Thoracic Root.—Muscles of flank and abdomen contract; flexion of hip, but not regularly or in all individuals.

XIth Thoracic Root.—Muscles of flank and abdomen, and intercostal space, with stimuli of moderate strength, never any movement in limb in any experiment.

VIIth Thoracic Root.—Muscles of back and side of chest; some of superficial more readily than the intercostals. The intercostals most readily caused to contract are those of the 7th and 8th spaces and after them in 6th space. It is almost impossible to evoke contraction in the crossed intercostals; no movement in limbs.

Vth Thoracic Root.—Muscles of back and side of chest, intercostal spaces chiefly involved are of 5th and 6th spaces; no movement in limb except occasional retraction of shoulder.

IVth Thoracic Root.—Retraction of shoulder; dilatation of pupil confined, or almost so, to the eye on the side stimulated; occasionally contraction of part of triceps.

IIIrd Thoracic Root.—Retraction of shoulder; contraction in part of triceps occasionally well marked; occasionally flexion and adduction of thumb, with less commonly slight flexion of other digits; dilatation of same side pupil.

IInd Thoracic Root.—Movement in shoulder; slight flexion of thumb and digits;

sometimes contraction in part of triceps. [Dilatation of pupil of same side.—July, 1897, C. S. S.]

Ist Thoracic Root.—Movement of shoulder, certainly retraction sometimes, with contraction in part of triceps; adduction and flexion of thumb and flexion of other digits; extension of elbow, sometimes flexion of elbow; less easily slight flexion, and some pronation, of the wrist. This root on being examined in three (anterior, middle, and posterior) sets of filaments elicited the same replies from each of the sets, except that flexion of the elbow was less unfrequent from the anterior than from the posterior.

VIIIth Cervical Root.—Adduction and flexion of thumb, flexion of other digits, flexion, more often extension of wrist, sometimes with drawing to ulnar side; drawing in and down of shoulder, retraction of upper arm, with occasional contraction in part of triceps going from humerus to scapula. At elbow rarely extension, sometimes flexion, during the former movement the triceps was seen to act, during the latter movement the supinator longus, but the biceps very little. When the examination was conducted on the root in three divisions, extension and triceps action were less common from the anterior than from the posterior, supinator longus action and flexion more common from the anterior than from the posterior.

VIIth Cervical Root.—Adduction and flexion of thumb and flexion of other digits; flexion of elbow, retraction of shoulder. By examination of this root in three sets of filaments, the reply obtained from the lowest was frequently flexion of digits, followed by flexion of elbow, while reply from anterior set was frequently flexion of elbow followed by flexion of digits. Extension of elbow replacing the more usual flexion of elbow is very unusual from this root.

VIth Cervical Root.—Flexion of elbow; adduction and flexion of thumb, less frequently with flexion of the other digits; drawing back of shoulder, but less marked.

Vth Cervical Root.—Flexion of elbow; movement of shoulder, sometimes retraction, sometimes a drawing-up; adduction and flexion of thumb, less frequently of other digits as well. Retraction of shoulder, when it occurs, is not so well marked as at lower root; it is sometimes a simple adduction toward spinal column.

IVth Cervical Root.—Retraction of shoulder, or else protraction and lifting of shoulder: flexion of elbow, not invariable, occasionally flexion and adduction of thumb with or without flexion of other digits; lateral flexion of neck.

IIIrd Cervical Root.—Elevation of shoulder; drawing down of same side of head; flexion of elbow feeble and occasional. The flexion of elbow from this and preceding roots was always, in great measure, supinator longus action. Twisting of head and neck to opposite side.

IInd Cervical Root.—Drawing up of shoulder, down of head on same side; turning of chin toward opposite shoulder with neck. Neither in this root nor in preceding did moderate stimuli evoke contraction in the muscles of the hyoid region.

Vth Cranial Nerve.—Opening of mouth; turning of chin toward opposite shoulder; wrinkling of muzzle; conjunctival reflex.

The above results possess points of interest, but it must not be forgotten the value of a reflex obtained by exciting the afferent spinal root, or one of its filaments, is but slight as regards the light thrown by it on the normal working of the spinal cord. It is only truly estimated when it is remembered that the Mammalian spinal root is not a functional combination but a morphological one.* To stimulate the whole of one single afferent root by itself is to do what in Nature never normally occurs. So also to stimulate one continuous half or fourth of such a root, is to do what is never done naturally. The end of a penholder pressed upon the skin anywhere—at least, anywhere on the limbs—excites contemporaneously single nerve fibres scattered through two consecutive (in many cases three consecutive) spinal afferent roots. Experiments on the roots are suitable at the commencement of an investigation of the spinal reflex actions, because the roots, more readily than the peripheral nerves, provoke reflexes (*vide infra*), and the experiments are, therefore, easier to perform; but they are less valuable in their physiological results, because the accompanying conditions are less known and less controlled. The *root* reflexes, to be of use for the understanding of the working of the cord, must be considered in collation with peripheral nerve reflexes and with skin-spot reflexes. For that reason I shall not consider them alone here, but later with the other reflexes obtained.

Spinal Shock.

Here it is necessary not to forget the possibility—indeed, certainty—that by cutting out long neural paths either by spinal transection or by certain depths of chemical anæsthetisation, the various intraspinal paths and resistances are not merely altered, but altered unequally. It is imperative, therefore, here, to consider the phenomenon of "shock"; I do so the more willingly, because this condition has, as I think, received as yet hardly adequate attention from physiologists.

"Shock," like "collapse," is a term more used by the clinician than by the physiologist; the scope of both words is usually left ill-defined. In some forms of the clinical condition circulatory disturbance and inspissation of the blood play a part in "shock," but as understood by the physiologist, "shock" is primarily a nervous condition. "If in a Frog the spinal marrow be divided just below the occiput, there

* SHERRINGTON, 'Journ. of Physiol.,' vol. 13, 1892.

are for a very short time no diastaltic actions in the extremities. The diastaltic actions speedily return. This phenomenon is 'shock.'"* In this, as in previous papers, I myself mean by the term *the whole of that depression or suppression of nervous reaction which ensues forthwith upon a mechanical injury of some part of the nervous system, and is of temporary nature.* The best explicit account of the condition is contained in the papers of GOLTZ. By him temporary paralysis following injuries of the brain or cord are all classed as *Hemmungserscheinungen*, and these collectively may be considered to compose the phenomenon of "shock." GOLTZ'S† descriptions of spinal shock are masterly, but they refer entirely to the Dog, and to transection below the middle of the back. As it is in the Monkey that the phenomenon appears at maximum, and especially consequently to high cervical transsection, I shall give a description of it as so seen. No more remarkable nervous condition can be imagined.

Whether the position of the severance be near the top or at the bottom of the thoracic region makes some, but no very great, difference to the general result, beyond of course increasing or reducing the *number* of spinal segments displaying the phenomenon. The "shock" appears to take effect in a *downward* direction only. Thus section below the brachial enlargement does not obviously disturb in any way the reactions of the upper limb, and this, although we know by anatomy (Wallerian method) that the number of upward channels ruptured by such a section is enormous, and must think, therefore, that many co-ordinating ties between the upper and lower limbs are destroyed. Again, most striking instances of the absence of upward spread of the depression due to "shock" are afforded by transections abutting on the lower edge of the 5th cervical segment; these depress the respiratory activity of the phrenic motor neurons hardly at all even momentarily (Cat). The rhythmic action of the motor neurons (for the diaphragm) is not obviously interfered with, although on the lower side of the transection depression may be profound. Analogously, the sudden cutting off of that stream of subconscious centripetal impulses which must be continually pouring to the brain from tail, lower limbs and trunk, seems to disturb the head and brain not at all. The animal immediately after the section will direct its attention to catching flies, or looking out of the window, taking no notice of nor apparent interest in its paralysed and insensitive parts. After section of the cord above the 1st cervical pair there is no obvious disturbance in the head; as the creatures lie quiet and watchful, the only and dubious sign of abnormality is a tendency to drop off rapidly and frequently into sleep. The pupils are equal and, of course, small.

If after transection above the 1st cervical level in the Cat sufficient time be allowed for the first effects of shock to pass away, the condition of the reflexes in the limbs,

* MARSHAL HALL, 'Synopsis of the Diastaltic Nervous System,' London, 1850.

† PFLÜGER'S 'Archiv.,' vol. 8, 460. "Die functionen des Lenden markes des Hundes."

both fore and hind, be examined, and if then the cord be a second time transected, and this time at the 6th thoracic level, the second section produces a shock effect but only on the aboral side of it. In the lower limb the skin reflexes, which may have been numerous and of sustained discharge, become few and brief, *e.g.*, at the ankle, instead of an alternating discharge of dorsal and plantar flexors, the idio-lateral reflex may be reduced to a simple dorsal flexion. In the fore-limbs, on the contrary, exaltation has occurred: the skin reflexes are more numerous and more sustained. The crossed reflex (in my experience rarely obtained) from one fore-limb to the other, may become elicitable, although not so previously. Similarly in front of the top section signs of exaltation are present. The surface seems hyperæsthetic; a single touch with a piece of paper on the snout elicits vigorous licking of the spot touched; the mere approach of a hot water can (used to keep the animal warm) evokes screwing up of the eyes and of the mouth; salivation is profuse, as a rule; a touch on the vibrissæ evokes exaggerated facial movement; I have seen photophobia.

The downward, posterior, aboral direction in which shock takes effect is, although the opposite of the direction of the vast majority of the fibres of the great afferent column of the cord, the same as that of easiest spread, both of the short and long paths that are intraspinal in the sense of confined in their course to the limits of the cord itself. The ground for this, which is contrary to the "law" of PFLÜGER, will be given on a later page. It will be seen that PFLÜGER'S "laws" must be modified in various particulars (see below pp. 170–175).

After transection at the top of the cord there appears to be more shock in the fore than in the hind limbs. Long path reflexes are less able to evoke movement from the fore-limbs than from the hind, *e.g.*, stimulation of pinna of ear more easily evokes movement of foot than of hand. Also the reflex movements obtained from each limb by excitations incident on itself are movements less forcible than those elicitable from the hind-limb. Occasionally, stimuli applied to the fore-limb evoke no movement in itself, though a brisk movement in the fellow hind-limb. The reflexes obtained under these conditions from the fore-limb, especially of flexion of elbow, tend to be tonic rather than clonic, whereas clonic contractions are the rule in the hind-limb, but this may depend on something other than depression. The depression of reflex activity after high cervical transverse section might be supposed to be due to the fall in general arterial blood-pressure which must ensue. That this cannot be the chief part of the explanation of this shock is clear from the above considerations: (1) that the head does not participate in the "shock," although participating in the lowered blood-pressure; and (2) that when the transection is in lower dorsal region, the "shock" distal to the sections is about as severe as after cervical transection. Besides, OWSJANNIKOW* pointed out that section of the

* LUDWIG'S 'Arbeiten,' 1874, p. 314.

splanchnics and its accompanying fall of blood does not cause shock, and that excitation of the peripheral ends of the cut splanchnics and the production of a good arterial pressure does not set it aside.

Paraplegia from Spinal Transection in the Ape.

In the Monkey in some instances three-quarters of an hour or so after transection below the region of the brachial enlargement, a *status* supervenes in which with cold hands and ears the animal lies down listless, and perhaps unconscious, with respiratory movements of the CHEYNE-STOKES type. This state may persist twelve hours or so, and end either in gradual recovery or death. In most Monkeys this condition does not occur. I have never met it consequent to similar operations in the Cat or Dog. It has nothing to do with the surgical progress of the wound, which is trifling in extent, and heals readily. It is usual for the rectal temperature to fall a degree or more immediately after section of the cord in the thoracic region.

As regards the nervous reactions elicitable from the isolated length of cord, for about twenty minutes after the performance of the severance, neither by mechanical, thermal, nor electrical excitation of the skin innervated from below the point of severance, can any reflex movement at all be elicited. The one exception to this is occasionally the so-called crossed knee-jerk, which, unlike the direct knee-jerk, is—to judge by the length of its reaction time (BURCKHARDT)*—a true reflex. It may appear strange that a "crossed reflex" should be thus early among the reflexes to appear. I find on examination that the reflex is not in reality a "crossed reflex," a statement which is amplified below, p. 176. After the brief interval certain skin-reflexes begin to appear; almost always earliest is adduction-flexion of the hallux, elicitable by stimuli applied to the 3rd, 4th, or 5th digits (plantar surface or sides), or to the skin of the sole, especially of the fibular side. The movement obtained from the hallux is often tremulent. Similarly, after section above the brachial enlargement, the earliest skin-reflex to appear is usually flexion and adduction of the thumb on stimulation of the palmar surface, or sides of the little 4th or 3rd fingers, or of the palm, especially in its ulnar part. A little later, or equally soon in some instances, appears feeble movement (generally protrusion) of the anus in response to stimulation in the perineal region; also feeble abduction of the tail in response to stimulation in the perineal region, or of the ventral surface of the tail itself; also, further, movement (usually flexion, sometimes extension, sometimes abduction, especially of index) of the digits, in accompaniment to that of the hallux (or pollex) on excitation of the plantar (or palmar) surface, generally excluding, however, the skin of the hallux (or pollex) itself.

* GOTTLIEB BURCKHARDT, "Uber Sehnenreflexe," 'Festschrift dem Andenken an ALB. v. HALLER dargebracht.' Bern, 1877, pp. 4–37.

Usually somewhat later, a slight contraction of the hamstring or gracilis muscles —at first often of the inner hamstrings only—becomes elicitable by severe excitation of the sole, and generally of no other region than the sole. All this time the limbs hang limp and flaccid, without any sign of spasm, except not infrequently fine feeble irregular twitching of the hallux (or pollex), sometimes of the other digits as well. The foot is warm. In these experiments, when reflexes were to be evoked from the skin, care should be always taken to maintain the temperature of the skin. As to the knee-jerk, this phenomenon, not truly reflex yet intimately dependent on the reflex tonus of the *crureus* and *vastus internus*, in many instances is elicitable for a few seconds immediately following the severance of the cord, but then disappears, to reappear only in the course of days or even weeks.* In some Monkeys, however, as in the Cat and Dog, the knee-jerks are not even temporarily abolished by the section. I have seen them maintained both after section as high as the Ist cervical segment and as low as the Ist post-thoracic segment.

The reflex reactions may remain in the just-described condition of paucity and depression for many hours and for many days; in this a striking and significant contrast exists between the Monkey on one hand, and the Cat and Dog upon the other. The sphincter ani, however, possesses some tone, and is not relaxed. There is no marked trouble with defæcation; but, after section at a low level, I have seen retention and dribbling overflow of urine, and the bladder may have to be evacuated by a catheter. In the course of time the action of the bladder, if lost at first, is regained, and further reflex movements usually become obtainable. A drawing up of the leg by the flexors of the hip and knee can generally be best evoked by pressing the foot or applying a cold sponge to the sole. A feeble wag of the tail can be obtained by pinching it. Flexion and adduction of the hallux become elicitable from a much wider area than formerly, from the whole foot, from the inside of the thigh, and from the end of the penis. The movement of hallux is usually associated with flexion of the other digits, also curiously often with extension of the other digits, an interesting movement which I have frequently obtained by excitation of the appropriate region of the cortex. The "cremaster" reflexes can be obtained.

In one young *M. sinicus* on the 14th day after the section a bilateral reflex appeared, and remained regularly elicitable for four months; on pinching the prepuce, both great toes were strongly flexed and adducted, both knees were slightly extended, and at the same time, by apparently a slight action of the flexors of the hips, thrust forward; the smaller digits were generally slightly flexed together with the hallux. I have seen a similar reflex from one other male, but only from one. I have never seen it in the female, the nearest approach being flexion of the hallux as an accompaniment of depression of the tail and protrusion of the anus in response to stimulation of the skin near the ventral commissure of the vagina. In the Cat I have seen

* SHERRINGTON, 'Journ. of Physiol.,' vol. 13, pp. 666–672.

bilateral movement (sometimes extension, sometimes flexion) of the ankles in response to irritation of the labium.

Abduction of the tail from its median symmetrical position is easily obtained, generally from a large area including the perineum, back of sacrum, back of thigh, and even the soles of the feet. The abduction is not unfrequently in a direction away from the side stimulated; that is to say, crossed reflexes are not uncommon; this often happens in the sense that, after excitation of the left side of the perineum has evoked abduction of the tail toward the left, excitation of the right side of the perineum evokes similarly abduction toward the left. Sometimes the crossed movement is elicitable without any previous "*bahnung.*"

As time goes on, the "drawing up" movement of the limb can be obtained from a larger area than at first; the calf, the outer side and back of the thigh, the skin lateral to the callosity and of the gluteal region near the root of the tail, not however as far inward as the median line, all yield it. The flexion of knee is not always carried out by the same muscles, thus, the inner hamstrings and often the gracilis seem to play a predominant part when the skin stimulated is of foot or leg, the outer hamstring when the middle or back of thigh. I have seen flexion of the knees with abduction of the thighs result from stimulation of the entrance to the vagina. Depression of the tail is elicitable from the skin above the ischial callosity. Defæcation can be sometimes induced by stimulation of the anal opening; it is accompanied by elevation of the tail and to and fro and side to side movement of it. A curving downward of the end of the tail is obtainable as an isolated movement from the skin of the ventral surface of the tail distal to the root. Protrusion of the anus is elicitable from a large field, *i.e.*, from the perineum around the anus and along the side of the vaginal orifice, also from over the back of the sacrum up to, but not beyond, the position of my *dorsal line** of the limb, and from the extreme top of the inner aspect of the thigh, near the raphe and beside the pubic fold. There and along its lateral border, this anal reflex field overlaps the reflex field of the hallux.

Flexion of the hip, apparently unaccompanied by flexion of the knee, comes to be elicitable from the femoral triangle, and, broadly speaking, from the whole front of the thigh; not infrequently associated with this *flexion of the hip* is adduction, and also adduction with slight *extension of the opposite* knee.

From the tibial side of the sole and hallux inversion of the foot, never, perhaps, as an isolated movement, generally associated to flexion of hallux with movement of the other digits, may be elicitable. From the fibular side of the sole, and from the small digits, eversion of the foot, never as an isolated movement, but generally associated to digital movement. Similarly, in the forearm, excitation of the skin of the little finger sometimes elicits some pronation with the flexion of elbow, while

* See above, Section III.

from the thumb some supination with the flexion of elbow is usual. Primary dorsal, more often than primary plantar flexion of ankle accompanies flexion of knee. Flexion of hip, more often than extension of hip goes with flexion of knee. Extension of knee is a movement of such rare occurrence as to be, as a local homonymous reflex,* hardly seen in most Cats and Monkeys in my experience. Adduction of the hip is much less uncommon, and among crossed reflexes is common ; in one animal it was regularly elicitable without other movement, or with slight extension of knee, as a crossed reflex from the skin near the raphe and pubic fold. It is not unfrequent to find that from some part of the sole can be evoked flexion of the small digits even when from most of the sole extension of them (at the metatarso-phalangeal joints) is elicited; generally the area for flexion lies on the fibular side of the sole.

The above stated degree and multiformity of reflex action having been attained, feeble and poverty-stricken as it is, I have never seen any further progress made. The longest periods through which I have maintained individual experiment have been *six months* and *five months* respectively. Not a little surprising is it to find that the movement which, on account of its being the most easily evoked and the one evoked alone when depression of reflex activity is great, may be called the primary spinal reflex of the limb, is the very movement which has been often urged to be *par excellence* the most eminently cortical one, namely flexion adduction of hallux. I have previously drawn attention to this significant fact.† Similarly in the fore limb, flexion-adduction of thumb, though often instanced as an action of peculiarly cortical nature, is really the most frequent and facile pure spinal reflex of the upper extremity. Its large and predominant representation in the cortex is concomitant with, rather than in contrast against, a large and predominant representation in the spinal cord. So also in the wry-neck reflex obtainable from Vth cranial nerve, and especially from IInd and IIIrd cervical roots, the movement, a turning of the chin and neck (with some lateral rotation of the head) away from the side of excitation, we have another example of a movement preponderantly represented in wide regions of the cortex (FERRIER, from frontal cortex ; SCHÄFER, from occipital cortex), also preponderantly represented in an extensive set of bulbospinal reflex mechanisms.

An almost invariable sequence to transection is eventually ulceration in the neighbourhood of the outer malleolus. The ulcers heal readily if dressed ; but they recur : I find no evidence for believing them due to trophic disturbance. They seem the result of pressure during the paralytic condition of the limb. Œdema of the foot also occurs. The muscles waste greatly, especially, I think, the quadriceps extensor of thigh.

* *i.e.*, a reflex elicited by excitation of the limb itself.

† 'Journ. of Physiol.,' vol. 13, p. 621, 1892.

A fact of importance is that if regularly repeated passive extensions be not undertaken and kept up, "*late rigidity*" "contracture" ultimately flexes the hips and knees. The onset of the rigidity is shown by resistance to movement in the direction toward which act the muscles antagonistic to those becoming rigid: this can be in some cases felt in two or three weeks. The atrophy is severest in the extensors of the knee, at least that is my experience in the Cat, Dog, and Monkey. I cannot confirm FREUSBERG* when he states there is to be found in the dog no alteration in the nutritive condition of any of the muscles. Myself, I find it affect both sets of muscles, flexor and extensor; much as MUNK† describes after cortical ablations, when hemiplegic contracture occurs in the Monkey. That the rigidity "*contracture*" affects in the lower limb the flexors in the Monkey, rather than the extensors, as I am told is the case in Man, may be due to extension of the limb being more predominant in the erect position than in the quadrupedal.

In some of the Monkeys with hind-limbs insensitised by spinal transection, the animals attacked the insentient limb: they began to pull it literally to pieces with an air suggesting playful curiosity. In one case the great sciatic nerve at the hip was frayed out and through in the course of a forenoon. In our research on the effect of rendering the limb insentient (apæsthete) by section of its afferent nerve roots, Dr. MOTT and myself met with a similar experience in some individual animals.‡ The ataxic and semi-paralytic condition of the limb evidently annoys the creature although not causing it pain.

The amount of reflex movement elicitable, after spinal transection, varies much in different monkeys of the same species: also in one and the same individual from day to day. On some mornings mere vestiges of reflexes obtainable on the previous morning might be all that were possible. In most cases a few repetitions tires out the reflex reaction; after increasing somewhat for a few repetitions at the beginning of the examination, they begin to fade out, and do so unless a rest is allowed. To increase the intensity of the stimulation is not of much avail, *the reflex arc behaves somewhat like cardiac muscle in responding its approximate best or not at all if the stimulus applied be not subliminal.*

The *discontinuance* of a prolonged stimulation, especially when it is itself becoming inefficient, I have very often found provoke a fresh outburst of reflex activity. HEAD§ and FREUSBERG|| have pointed out the same thing. I have seen it with faradic and with mechanical stimuli. After stretching a muscle from its tendon steadily and then suddenly relaxing it, the relaxation often causes a sudden fresh outburst of movement, *a terminal discharge.*

* PFLÜGER'S 'Archiv,' vol. 9, 1875.

† H. MUNK, 'Sitzungsber. der Königl. Akad. der Wissensch. zu Berlin,' 1894.

‡ 'Proc. Roy. Soc.,' vol. 57, p. 481, 1895.

§ 'Journ. of Physiology,' vol. 10, p. 1, 1889.

|| PFLÜGER'S 'Archiv,' vol. 9, p. 372, 1874.

In the Dog, soon after the performance of transection, vigorous reflex movements can be easily obtained; especially in the hind limbs and tail; these have been known and their vigour and variety appreciated since the papers by MARSHALL HALL,* LONGET,† BRACHET,‡ CAYRADE,§ GOLTZ|| and FREUSBERG, and especially by the papers of the two last-named observers. From my account above given of the Monkey it will be seen, therefore, that there exists a difference between the condition of Monkey and of Cat and Dog in regard to reflex play in the spinal cord after spinal transection. To meet so great a physiological contrast between these two Mammalian types is surprising: the difference is distinctly great. I do not, however, believe it a really profound difference; it is, I think I shall show, quantitative rather than qualitative. But it is nevertheless great and significant. One may almost say the Dog in this respect seems to differ less from the Frog than does the *Macaque* from the Dog, although the morphological gap between the two latter is so much less than between the former. In the Dog and Cat the spinal reflex movements are more forcible, more prolonged, more readily obtained, and less easily exhausted by fatigue. In the Cat and Dog it is not unusual to see the hindquarters raise themselves reflexly—with superficial similitude to willed movement—from the sitting to the standing posture; this powerful reflex, described by GOLTZ, often occurs when the animal moves on being encouraged to stand up. In the Monkey, on the other hand, the hind limbs hang helpless, with a lethargy comparable to deep stupor. The few feeble abortive movements above described are difficult to arouse and sometimes not elicitable at all. It might, perhaps, have been anticipated that in the Monkey, with its wealth of range and scope of limb movement, compared with which the hind limbs of the dog are little more than props, the reflex spinal machinery would have exhibited conformably a more multiform and surpassing co-ordination than in the Cat and Dog. "Shock" once over, spinal reflexes might have been expected more various than those of other animals. Such a supposition is dispelled by actual experiment, as far as all cutaneous reflexes are concerned, although it is true that the variety of homonymous reflex about the knee of the Monkey appears slightly greater than at knee in the other species.

On the other hand the difference between the variety and even the extent of the spinal reflexes obtainable from Cat and Dog on the one part and from *Macacus* on the other, is much diminished when, instead of skin and nerve-trunk, the spinal roots proximal to their ganglia are stimulated. The direction and muscular composition of the primary movements elicitable by faradic excitations of the afferent spinal roots themselves are in Cat, Dog, and Monkey, especially in the hind limb region,

* 'Memoirs on the Nervous System.' London, 1837–1852. 4to., London.

† 'Traité de Physiol.,' vol. 2, p. 241.

‡ 'Recherches expérim. sur les Fonctions des Systèm. Nerveux ganglion,' Paris, 1839.

§ 'Le Mouvement Réflexe. Thèse pour le doct. en méd.' Paris, 1864.

|| PFLÜGER'S 'Archiv,' vol. 8, p. 460, 1873.

almost the same for all three types. The spinal machinery for movement is therefore actually present in the Monkey as in the other two, and indeed, as was expected, appears to be more complex. But it is more difficult to set in motion and to keep going. This question requires further appeal to the phenomena of "shock."

As was to be expected, shock is more severe and lasting in the Monkey than in the other laboratory types, and its symptoms are more profound and prolonged than in any other animal I have observed. The symptoms of shock, in many monkeys, persist for days instead of hours or minutes, as in Cat and Dog. It is important to note that in the Monkey, much of what we are, from observations upon the lower animal types, inclined to regard as temporary and relegate to block or "shock," in GOLTZ's language "*Hemmungserscheinungen*"—not "*Ausfallserscheinungen*"—proves, under prolonged observation, to be, I must think, permanent; in fact, to be *true deficiency phenomenon.* Every histologist acquainted with the comparative structure of the spinal cord in the Ape and in the Dog, must have been impressed with the far greater complexity obvious in the former. The above evidence is in accord with that, for it shows that the same trauma inflicted upon the cord leads, in the monkey, to much heavier permanent defect than in the dog; just as, in fact, ablations of the cortex cerebri are pregnant with far greater "*Ausfallserscheinungen*" in the Monkey (FERRIER, H. MUNK, SCHÄFER, MOTT) than in the Dog (GOLTZ). It is reasonable to argue still severer results in the case of the human spinal cord; of which again we know the minute structure to be yet more complex still. *The permanent damage done is, therefore, as well as the initial shock, disproportionately greater in Monkey than in Cat and Dog.*

To return briefly for a moment to initial shock due to spinal section in the Monkey. There can hardly be witnessed a more striking phenomenon in the physiology of the nervous system. From the limp limbs, even if the knee-jerks be elicitable, no responsive movement, beyond perhaps a feeble tremulous adduction or bending of the thumb or hallux, can be evoked even by insults of a character severe in the extreme. That which the delicate yellow spot is to the sensifacient sheet of the retina, may the thumb and index be said to constitute in the great sensifacient field of the limb. Nevertheless, a hot iron laid right across thumb, index, and palm, remains an absolutely impotent excitant, or able only to evoke a faint flexion of the thumb; the crushing of a finger has no greater effect. A huge afferent nerve, such as the internal saphenous, containing some five thousand sensory nerve-fibres, when laid across the electrodes and subjected to currents absolutely unbearable upon the tongue, elicits no further response, and probably no movement whatsoever. To the whole popliteal nerve representing an area of sentient skin which includes the entire sole and much of the leg besides, intolerable faradisation can be applied and elicits no more, and often even less, response. A more impassable condition of block, or torpor, can hardly be imagined: its depth of negation resembles, to superficial examination, profound chloroform poisoning. The circulation is, however, approximately normal in these cases; and the respiration absolutely so. The skin, as above stated, is well warm, even to the tips of the hands and feet. Further, the fundamental distinction between the condition and that induced by any chemical nervous depressant, is clear in the following two features. (1) The spinal motor neurons, though profoundly inaccessible to stimuli, applied *viâ* skin or afferent nerve-trunks, are perfectly open to any applied *viâ* the pyramidal paths: excitation of the pyramidal tract at the top of the cord evokes as readily as or more readily than ever, in both limbs, its usual variety of movements. (2) Excitation, mechanical or by weak electric currents quite imperceptible to the tongue, of the *central ends of the spinal posterior* (*dorsal, sensory*) *roots themselves, fairly readily evokes the usual reflex movements* elicitable—although enormously stronger stimuli fail absolutely when applied to the skin and afferent nerve-trunks. At first finding this, I supposed an explanation might lie in the fact that the roots contain large numbers of afferent fibres from muscles,* while the peripheral nerve-trunks and surfaces tried, are chiefly cutaneous; but excitation of the spinal end of the hamstring-nerve, with its quantities of afferent nerve-fibres from muscle and deep structures, caused no more effect; caused, in fact, less effect than a pure cutaneous sensory trunk, such as the long saphenous. This condition, although most usual and striking in the Monkey, and therefore here chiefly described in his case, is seen, to a certain extent, also in Cat and Dog. When, in them, the spinal depression is great, it is easily found to be more marked when examined by excitation of skin or peripheral nerves, than when examined by excitation of the afferent spinal roots; the motor reactions, provokable from the former, are less ample and less numerous than from the latter. It is no question of escape of exciting current to the motor roots themselves. Finally, this further point seems clear, from the above analysis of "shock," that the phenomenon is not resident, chiefly or indeed at all, in the peripheral sensory end-organs, or at their junctions with afferent neurons; because the peripheral nerve-trunks themselves are as inefficient as the skin, tendons, &c. My own experience leads me to think that the condition of a spinal cord isolated by a spinal transection is often more normal a few hours after the transection than it is when long periods of weeks and months are allowed to elapse. I am well aware that this is contrary to the opinion of GOLTZ and others. The advantage believed to accrue from waiting is that the phenomena of shock may have time to pass off as completely as possible. How long the phenomena of shock may last at longest is a question on which very different views are held. GOLTZ, to whose trenchant observations and bold system of experiment we owe so much of our knowledge of the physiology of the central nervous system, is the founder of a school which works in the belief that the phenomenon of shock may persist for months, even years. It is, as far as not, merely a matter of nomenclature, a question on which no definite decision seems as yet possible. I myself have

* SHERRINGTON, "On the Anatomical Constitution of the Nerves of Skeletal Muscles," 'Journ. of Physiol.,' vol. 17, 1894.

gradually been driven to the belief that "shock" does not take long to pass off, *i.e.*, does not at longest persist for more than a few days.* But though shock passes off, the alterations produced in the isolated cord or piece of cord (by permanent withdrawal of the influences it has lived accustomed to receive from other portions of the central nervous system), progress, and are in a sense cumulative. The decreasing depression merges—at present inextricably for us—in the increasing onset of an "isolation-alteration."† Much of what is called "shock," in regard to the Mammalian cord, is, I believe, due to "isolation-alteration," and is really permanent, that is to say, would not pass away if the animal were to live healthily for any number of years. The most favourable time for the examination of the independent capabilities of the spinal cord is that when the sum of "shock" and "isolation-alteration" together is of smallest amount. That time compounded as it is of two such variable factors is itself extraordinarily variable. In result of spinal transection in Monkey, I am sure that "shock" lasts longer, and that "isolation-alteration" comes on earlier than in the other animal types commonly observed in the laboratory. It is the conjunction of the periods of these two phenomena which renders so difficult and so largely defeats attempts at observations on proper spinal reactions of the Monkey. If the overlap of the two is great, then no spinal reflexes, or only the merest traces of them, may be observable. In Man it is only natural to suppose—and what clinical experience I have had access to strengthens me in the belief—that even more than in Monkey will "shock" be protracted, and "isolation-alteration" speedy and severe. The observations of BASTIAN‡, BOWLBY§, and BRUNS‖ teach us that the clinical picture of the effects of total transverse lesions of the human spinal cord does not accord in the way that medical text-books have been wont to describe with the long-known results obtained from the transected cord by the physiologist. Older physiological experiments are, however, not based on nervous systems so approximate to the human as is that of *Macacus, Cercocebus*, &c. Of these latter I would say that their condition after spinal transection commonly resembles in its features in the most striking manner the condition of spinal depression observable after transverse spinal lesion in Man, and considered by BASTIAN to be the typical status.

My results on Monkeys bear out strikingly and fully what BASTIAN describes as the

* I am not considering here the complications arising out of long, badly healing and suppurative wounds, and the continual irritation they may produce if situate in the nervous system. Such conditions no longer, thanks to LISTER, complicate the lesions of experimental physiology.

† MUNK'S "Isolations-änderung," a term which expresses what I mean, has been introduced by him to denote alteration resulting from a lesion of cortex cerebri. I venture to introduce the word in the above wider sense.

‡ 'Medico-Chirurgical Transactions,' 1891. London.

§ *Ibid.*

‖ 'Neurologisches Centralblatt.' Berlin, 1893.

typical condition in Man after complete transverse destruction across the cord. The chief difference is that in the Monkey in most cases—partly, perhaps, because the lesion is more localised by experimental infliction than by accidental—the depression is not so severe. For instance, the knee-jerk, which disappears almost immediately after the transection, returns usually in a week or ten days,* often, however, not for three weeks; occasionally, on the other hand, in ten minutes.

Rules observable in Spinal Reflex Actions.

I will now attempt to state and illustrate such rules of reflex action as seem capable of induction from the above observations. In the first series of the following pages I shall refer only to reflexes of short path, *i.e.*, to short spinal reflexes.

In doing this use must be made of the terms "spinal segment," "short spinal reflexes," "long spinal reflexes," and "spinal regions." The spinal segment is often loosely, though arbitrarily, laid down to be a fraction of spinal cord included between two imaginary frontal sections, placed one on each side of a nerve-pair, and each half-way between the next pair below and the next above. Neither morphologically nor physiologically does this cylindroid mass of the cord merit the term "spinal segment." To take such a fraction as representing either a structural or a functional unit or spinal link, from a series of which the cord is built up by concatenation, is to ignore one of the most important characters of construction of the myelon. Overlapping and inlapping of segments exist in the segmental arrangement of the cord itself just as in the segmental arrangement of the neurons in the body-metameres outside. The "block" delimitation of the spinal segment is no longer defensible or useful. It omits structures which are essential components of every complete spinal segment; it includes much that is extraneous. It is applicable, probably, to one set only of the spinal neurons, namely, to the motor neurons, for, as I† and A. S. GRÜNBAUM† have shown, the spinal motor root is of strictly local origin.

The extent of intra-spinal attachment is very different in the two cases of the dorsal (afferent) and of the ventral (efferent) root respectively. The former overlaps a *series* of the latter. If, for mere convenience of statement, the *surface* attachment only of the roots is considered in the definition "segment" there remains, apart from the obvious artificiality of the postulate, still a difficulty with the dorsal (afferent) root. This difficulty lies in the frequency with which the filaments of dorsal roots trespass upon each other's territory, a filament from one root ganglion not uncommonly joining a filament from the next ganglion to plunge together with it into the postero-lateral fissure of the cord. Not very rarely a filament on issuing from the ganglion pursues an oblique course (generally in my experience *downward*) across a part, or

* SHERRINGTON, 'Journ. of Physiol.,' 13, 1892; A. S. F. GRÜNBAUM, 'Journ. of Physiol.,' 16, p. 368.

† 'The Journal of Physiology,' vol. 13, p. 707, 1892; vol. 14, p. 300, 1893; vol. 16, p. 368, 1894.

even the whole of the filaments from the next ganglion to enter the cord among or even subjacent to them.

Example.—I recollect noting in the human brachial enlargement a filament from the VIIth cervical ganglion plunging into the cord half-way down the series of filaments from the VIIIth ganglion. I believe such variations are not found in the filaments of anterior roots. I have myself, with considerable opportunity for search, never yet found any.

The surface attachment of the dorsal (afferent) root is, therefore, just as its deep attachment, a less reliable segmental guide than that of the ventral (efferent) root. But the collection of cells composing the spinal ganglion is a segmental collection, just as the collection of the intra-spinal neurons of the efferent root is a segmental group; indeed, the two are segmentally equivalent. To include in the "spinal segment" the cells of one root, and to omit those of the other, is obviously artificial and inconsequent. The spinal segment is, therefore, in this paper understood to include the neurons of the spinal ganglion, as well as those of the corresponding ventral (efferent) root, and along with these all other intra-spinal neurons whose cell-bodies lie between the same frontal levels as the neurons of the efferent root in question. I omit reference to the ganglia of the sympathetic, this paper not being immediately concerned with them.

As to "short paths," KÖLLIKER* defines them as paths which do not extend the whole length of the spinal cord and do not extend into the brain. I would propose to limit the term further. The reflex apparatus of the cord may be usefully considered in five regions, for the (1) tail, (2) pelvic limb, (3) trunk, (4) brachial limb, and (5) neck, each of these regions being double, because made of right and left component regions. I would consider "short" any paths which are entirely confined to a single one of these main regions. These main regions I separate as "spinal regions," on account of their each possessing a certain degree of physiological solidarity.

Short Spinal Reflexes.

The following rules refer almost exclusively to spinal reflexes of short paths only—*i.e.*, to "short spinal reflexes"—as understood by the above given definition.

Among inferences that may be drawn from the observations stated above one dealing with the degree of correspondence between the morphological structure and the functional mechanism of the cord may be taken first. Broadly speaking, it may be said that *the degree of reflex spinal intimacy between segments is directly proportional to their segmental proximity.*

The fundamental experiment which illustrates this rule is the following:—Cat, the cord transected at the Ist cervical level; the roots of the VIIth thoracic nerve exposed in the vertebral canal; these severed together through the ganglion, well outside the dural sheath; the central end of the mixed nerve, *i.e.*, of both roots in the single sheath,

* 'Handbuch der Gewebelehre des Menschen,' 6th edit., vol. 2, 1st half. Leipzig 1893.

then ligated, held up free, and excited with faradic currents; reflex contraction of the intercostal muscles of the 8th and 6th spaces occurs, that of the 8th space is a little more easily obtained than that of the 6th space, *i.e.*, with slightly less intense currents. Pinching the central end of the nerve between ivory-tipped forceps also evokes contraction in the 6th and 8th spaces; by pinching 7th, it is usually not possible to evoke contraction in intercostal spaces further removed than 6th and 8th; by sufficient increase of intensity of the faradic currents a further spread is possible. By applying the electrodes to the cord itself along the dorso-lateral fissure in the region of entrance of the filaments of VIIth thoracic contraction of the muscles in the 8th and 6th spaces is easily produced, but not so easily in spaces further removed, though with less difficulty than by excitation of the root filaments of 7th outside. On shifting the electrodes to the line of surface origin of the filaments of the dorsal root of VIIIth thoracic, the contraction in the 6th intercostal space at once disappears; on shifting to the surface entrance of VIth thoracic, the contraction in the 8th space drops out, if not completely, very nearly so, but by increasing the intensity of excitation can be regained. The amount of intraspinal overlap would thus seem to be in this region about equal in both directions, and to start from the segment of the afferent root, excited as from a centre; but the direction of spread is somewhat easier away from the head than toward the head, a significant exception to the 4th "law" of PFLÜGER.* It may be recalled that it was proved in my previous paper that the sensory innervation of the skin of most of the trunk is segmentally anterior to the motor innervation of the underlying muscles, an oblique relationship existing between them. By carefully graduating the degree of excitation the course of the spread from one intercostal space to the next seems to be quite recognisably accompanied by increase of resistance of conduction.

The following are adduced as further examples of the rule of segmental proximity:—

Thus:—By excitation of the sole, flexion of hallux can be elicited more readily than protrusion of anus; from skin of perineum, conversely, protrusion of anus more readily than flexion of hallux, and this with prefixed plexus.

From IIIrd, IVth, Vth, and VIth cervical afferent roots, action of supinator longus is usually more facile than action of triceps; from VIIth cervical there is not so great a preponderance of one or other; from VIIIth cervical and the four highest thoracic roots, action of triceps is the more easily obtained as a rule.

In the Cat, active flexion of the knee is usually a more facile reflex than active flexion of hip in response to excitation of IXth, VIIIth, and VIIth post-thoracic afferent roots; but IInd, IIIrd, IVth, Vth, and VIth roots as readily yield flexion of hip as of knee, as a rule.

In *Macacus*, flexion of thumb and fingers is more readily obtained by excitation of the skin of the hand itself than of any other part of the limb; the VIIth and VIIIth cervical afferent roots and the Ist thoracic are those supplying the skin of the hand, and the motor root of each of these segments innervates the flexor muscles of the digits. A similar arrangement obtains between planta and hallux.

* 'Ueber die sensorischen Functionen d. Rückenmarks.' Berlin, 1853.

In the Cat, mechanical or thermal stimuli applied to the pad evoke primarily and most easily reflex flexion of the toes; this is true in fore-foot and in hind-foot.

In the Cat, either dorsal flexion or plantar flexion of ankle may be the reply to cutaneous stimuli on the foot, but dorso-flexion is the more usual, and is more certainly obtained from the dorsum pedis than from the sole, and least certainly obtained from the 4th toe. Now, the dorsum is supplied by sensory roots anterior to those supplying the sole, and especially to those supplying the 4th toe; *i.e.*, to the sole and to the 4th toe the IXth post-thoracic root sometimes, and the VIIIth always, contributes; to the dorsum, the VIIIth slightly, the IXth never, contributes; while the VIth contributes to the dorsum, but never to the sole and 4th toe, the VIIth being common to all. Now, dorsal flexors of ankle derive nerve-fibres from the VIth and VIIth roots chiefly, the plantar flexors from the VIIIth and VIIth chiefly.

In the Cat (and Monkey), reflex extension of hip is more readily obtained from the afferent roots posterior to the VIth (in Monkey Vth) than from the roots in front of VIIth (in Monkey VIth). The extensors of the hip receive their motor innervation chiefly from roots behind VIth (and Vth, Monkey).

Excitation of the outer side or edge of the sole evokes (both in Cat and Monkey), besides dorso-flexion at ankle, some tilting upward of that edge of the foot. This outward tilting is not elicited from the inner edge of the foot, inward tilting being then not unusual. Now, in the Cat, the outer edge of sole is supplied by VIIth + VIIIth ganglia (post-thoracic), while inner edge by VIth + VIIth; but outer edge is more richly supplied by VIIth than is inner edge. Now, peronei get motor neurons from VIIth and VIIIth motor roots, so that peroneal contraction might be expected to be stronger from outer edge than inner on the rule of segmental proximity. Same holds in Monkey on substituting roots V, VI, and VII for the above.

Dorso-flexion of ankle in Monkey is less easily obtained as a spinal reflex than flexion of the other hind-limb joints; the roots whence it is best obtained are the VIIth and the VIth. These are the sensory roots of the very segments which supply motor fibres to the pretibial and peroneal muscles.

The cremasteric reflex obtainable by scratching inner side of thigh and groin is obtained thus when, in Monkey, all the posterior roots of the region except IInd and IIIrd lumbar have been severed. It is also obtained by direct excitation of IIIrd lumbar root.

Extension of the hip and flexion of the knee can be with less difficulty provoked from the part of the outer aspect of the thigh behind my mid-dorsal line of the limb than from the region in front of it. As a further example may serve CAYRADE'S* observation that after mid-thoracic transection in the guinea-pig, pinching the root of tail causes flexion of the knee; stroking the belly adduction of hip and extension at knee.

This rule offers, I believe, especially when stimuli not far removed from minimal are employed, a useful key—as regards short paths—to many topographical relationships between field of excitation and field of reflex movement. Its existence is notable in face of the *oblique correlation* which was shown in my previous experiments,† to obtain over a large part of the trunk and limb between overlying skin innervation and underlying muscular innervation. The former being segmentally anterior to the latter, one might have expected that the sensory root of a spinal nerve would have evoked motor reply primarily from a segment a couple of metameres lower down in the segmental chain rather than from the motor neurons of its

* "Les Mouvements Réflexes," Thesis, Paris, 1864.

† 'Phil. Trans.,' B, vol. 184, p. 754.

own segmental level. I have, indeed, given evidence above, that in some regions the direction taken by "spread" does actually, to some extent, bear out the supposition suggested by the former paper; in other words, that contrary to PFLÜGER'S 4th law, the spread does not occur with greater facility in direction toward the brain, but rather, in some cases, with greater facility in direction from the brain. This downward tendency supports, not overrides, the rule; so that, indeed, from the rule of segmental proximity, another, which is its logical corollary, may be proceeded to. This is: *taken generally, for each afferent root there exists in its own spinal segment a reflex motor path of as little resistance as any open to it anywhere.*

Examples:—The adduction flexion of hallux elicitable with minimal stimuli from the VIIIth post-thoracic afferent root is obtainable with the same or even a lesser stimulus when the VIth, VIIth, and IXth post-thoracic motor roots are severed. (Monkey.)

Contraction of the hamstrings is elicitable from the VIth post-thoracic afferent root viâ the VIth post-thoracic motor root with an absolutely minimal stimulus. (Monkey.)

The afferent roots of the Vth, VIth, and VIIth cervical, and Ist thoracic nerves having been severed, excitation of the skin of the palm evokes flexion and adduction of the thumb; this response is not altered in character by subsequent section of the VIth and VIIth cervical and Ist and IInd thoracic motor roots. (Monkey.) A similar result to this is obtainable from the VIIth post-thoracic and the hallux. (Monkey.)

By minimal excitation of the long saphenous nerve flexion of the hip, due to fascialis and rectus internus, is elicited, and it is usually only by increasing the strength of stimulation that other muscles (*e.g.*, psoas and pectineus) co-operate with the above. The same result is seen when the Vth and IVth post-thoracic afferent roots have been severed. Now, I have pointed out in my previous paper that the fascialis is the only muscle in the lower limb supplied by one root only; that root is the VIth post-thoracic. Hence the internal saphenous, by its component from the VIth post-thoracic root, elicits contraction at least as easily as from any other, from a muscle whose motor innervation is through the corresponding (*i.e.*, VIth) motor root. (Cat.)

By minimal excitation of the IXth post-thoracic afferent root protrusion of the anus is usually more easily obtained than flexion of the digits, and this is so in prefixed plexuses in which the IXth motor root does not innervate any muscles of the limb. The anal reflex persists after section of the VIIth, VIIIth and Xth motor roots, *i.e.*, must have had a component through the IXth motor: the IXth afferent root, therefore, shows a slight preference for discharging into a motor centre present in its own segment as compared with another which is also open to it, but outside its own segment.

Minimal excitation of the VIth cervical afferent root elicits contraction of the supinator longus, while minimal excitation of VIIIth cervical afferent root elicits flexion and adduction of the hallux: motor fibres of the VIth cervical innervate the supinator longus, while motor fibres of the VIIIth cervical innervate the long and short muscles of the thumb.

Excitation (mechanical) of the Ist thoracic afferent root evokes usually flexion and adduction of thumb, but no dilatation of pupil; similar excitation of the IIIrd thoracic afferent root evokes usually well-marked dilatation of the pupil (almost exclusively homonymous), but no movement of thumb. The motor root of the Ist thoracic innervates thumb muscles but not the iris, while that of the IIIrd innervates the iris but not the thumb muscles (*Macacus*).

In the Monkey adduction-flexion of pollex and hallux, which are the most facile cutaneous reflexes of the whole limb, occurring when all others are absent, is provoked from the ulnar and fibular sides of palm and sole and from little digit easier than from elsewhere: ulnar and fibular sides of palm and sole are supplied by those spinal ganglia corresponding with the spinal segments possessing motor neurons for pollex and hallux. The skin of pollex and hallux themselves and of radial and tibial sides of palm and sole yield the reflex less readily; their skin is innervated from spinal levels segmentally less close to musculature of pollex and hallux.

In Monkey and in Cat excitation of the VIIth or VIIIth thoracic afferent root by absolutely minimal stimuli evokes often contraction in the muscles of the VIIth (or VIIIth) intercostal region and not in other intercostal: contraction in intercostal spaces other than VIIth (or VIIIth) is never obtained without contraction in that space.

An exception to this rule seems offered by the pinna: excitation of the pinna (Cat) evokes retraction of it; afferent nerves are Vth cranial, and Ist and IInd cervical. The motor nerve seems to be the VIIth cranial. The reflex continues well after section of the Vth cranial and Ist cervical; the reflex then involves discharge from the IInd cervical into the VIIth cranial, *i.e.*, the primary reflex is pluri-segmental.

Pluri-segmental Reflex Arcs of Low Resistance.

At the same time, as I have previously pointed out,* there co-exist for most afferent roots, together with their own uni-segmental paths of minimal resistance, other spinal reflex paths which extend beyond the limits of the afferent root's own segment, both upwards and downwards, and yet offer a resistance not with certainty demonstrable to be greater than that of the low resistance path confined to the one segment.

Examples: Stimulation of central end of palmar digital nerve on ulnar side of little finger evokes flexion and adduction of thumb. Similarly, excitation of palmar digital of radial side of index gives same movement. Section of VIIIth cervical afferent root does not obviously change the reflex. Section of the Ist thoracic motor root does not necessitate a stronger excitation of the little-finger nerve to evoke the movement. Section of the VIIth cervical motor root does not necessitate a stronger stimulation of the index digital to evoke the movement. Section of the IInd thoracic does not modify the reflex. Section of the motor root of VIIIth cervical finally abolishes the reflex, *i.e.*, the reflex flexion of thumb. The reflex path was not appreciably more resistant when it passed from Ist thoracic into VIIIth cervical or from VIIth cervical into VIIIth cervical than when confined entirely to Ist thoracic segment or to VIIth cervical segment.

Excitation of skin near orifice of vagina elicits protrusion of anus. The afferent roots of the Xth and VIIIth post thoracic nerves are now cut. Excitation, *i.e.*, a pinch of the skin as before, still elicits the protrusion of anus; the patent afferent root is therefore the IXth; the IXth ventral root is cut; a pinch as before still elicits the anal protrusion as readily as before. Similarly, using the roots of the opposite side in the same animal, excitation of the IXth post-thoracic afferent root with 20 k.s. just elicited anal protrusion, the motor root of IXth was then severed, whereupon IXth afferent root still evoked well a protrusion of anus. In the latter part of the experiment the possibility of a uni-segmental crossed reflex is eliminated.

For further examples reference can be made to my "Lumbo-sacral Plexus."

* 'Journ. of Physiol.,' 1892, *loc. cit.*

Functional Solidarity of the Motor Cell-groups for certain Groups of Muscles.

In such instances as these centripetal impulses poured into one spinal segment evoke centrifugal impulses in adjacent segments without demonstrably greater difficulty than when confined to the actual segment into which they were themselves thrown. Irradiation appears to meet with no increase of resistance when passing from one segment to another in these cases. The solidarity of these parts of the essentially segmented cord must be extraordinarily complete. The connection between the endings of the afferent fibres and motor cells of other segments may be as close as between them and *any* of the neurons. It follows that, in many instances at least, excitation of their own segment applied in minimal or approximately minimal degree to a single afferent root or of a fraction of a single afferent root evokes pluri-segmental "motor" discharge. Now I have shown that the group of motor neurons innervating a limb muscle, *e.g.*, flexor brevis, hallucis, or pollicis, is composed of individual neurons, belonging not merely to one but to two and three adjacent spinal segments.* From the above it is clear that the rule of segmental proximity does not operate to the extent of making motor neurons belonging to one segment in the pluri-segmental motor nucleus greatly more accessible by its own afferent root than are by that root the motor neurons of the other segments composing the nucleus; in fact they are only very slightly if in any degree more so. Here again facts lend no countenance to the assertion that the collection of fibres in each motor root represents one highly co-ordinate functional synergy. On the contrary they indicate that not the whole motor root, but particular fractional combinations of several motor roots are, in spinal reflex actions, to be considered units. The afferent channels of the cord treat the pluri-segmental motor stations or nuclei of these limb muscles as entities of homogeneous structure, as in fact physiological units.

From the foregoing it follows naturally that the reflex centrifugal discharge of the spinal cord is pluri-segmental. The rule may be stated thus: *in response to excitation even approximately minimal of a single afferent root, or even of a single filament of a single afferent root, the spinal discharge of centrifugal impulses evoked, tends to occur* viâ *more than one efferent root,* i.e., *is pluri-segmental.* It is interesting to note that this is more strongly the case in the limbs than in the thoracic region where the segments are less commingled. The segmental arrangement of the motor cells of the spinal cord is said by SCHWALBE† to be more obvious in the thoracic than in the limb regions. But in the limb region, the arrangement, if existent, consists of cell groups quite confluent at the boundaries of segments. I look upon the solidarity of the limb as structurally expressed by the pluri-segmental

* SHERRINGTON, 'Journ. of Physiol.,' vol. 13, p. 621, 1892.

† SCHWALBE, 'Lehrbuch der Neurol.,' 1881; also LÜDERITZ, 'Arch. für Anat. und Physiol.,' 1881.

character of the motor nuclei. KAISER'S* measurements lend no colour to SCHWALBE'S assertion of a segmental grouping of the motor cells. With care, the reflex discharge can, as above stated, be confined in the intercostal series to one segmental region, the spinal centrifugal discharge being then uni-segmental. This circumstance is in accord with the uni-segmental innervation of these muscles as compared with the pluri-segmental innervation of most limb muscles.

This serves to emphasise what I have frequently insisted on, namely, the physiological homogeneity of limb muscle and nerve-trunk, and the physiological heterogeneity, in spite of morphological unity, of the spinal nerve-root in the limb region; the spinal nerve-roots of the thoracic region are far less heterogeneous. The peripheral *nerve-trunk* is the *physiological* collection of nerve-fibres, *e.g.*, flexors collected together, vaso-dilators included with motors to muscles, &c. The *nerve-root* is the *morphological* collection, it contains, commingled into one, such heterogeneities as adductors of great toe, protrusors of anus, and vaso-dilators of the penis. Similarly with the skin, the median nerve-trunk supplies a patch of the palm that has obviously functional unity, but Ist thoracic nerve-root supplies such incongruities as the back and front of the little finger and of half the annulus and the tip of the olecranon process. It is *the formation of functional collections of nerve-fibres* (*peripheral nerve-trunks*) *out of morphological collections* (*nerve-roots*), which *is the explanation*—the meaning—*of the existence of limb-plexuses.* The reply to the oft-asked question what is the meaning and explanation of the distribution of the brachial and pelvic limb spinal nerves by plexuses, while the spinal nerves of the trunk region are not distributed by plexuses is, in my opinion, as follows:—In the trunk region the innervation of the muscles of the skin is as regards the distribution in them of the segmental nerves a system of comparatively slight overlap: the peripheral territory of each segmental nerve—especially each motor territory—is confluent with but does not mingle nearly so widely with the neighbour territories as in the limb regions. That is to say, in other words, each several area of skin and of muscle, especially of the latter, has in either of the limbs a more pluri-segmental spinal innervation than a comparable area in the trunk. The anatomical mode of innervating a definite area of tissue is, as we know, by means of collecting the nerve-fibres for the region into a nerve-trunk; where the innervation is pluri-segmental the nerve-trunk will therefore naturally be combined from components of several segmental nerves—where several such areas co-exist several pluri-segmental nerve-trunks will be formed and the separate segmental nerves will be split up into components, which become redistributed in the combinations which constitute the pluri-segmental nerve-trunks of the region—as, for instance, in the brachial region. The brachial and lumbo-sacral plexuses are an anatomical result of the greater degree of overlap, especially in the distribution of the motor part of their spinal nerves, obtaining in the limbs as compared with other, *e.g.*, the trunk region of the body.

* 'Ganglienzellen des Halsmarkes.' Haag, 1891.

Just as the motor spinal roots (apart from sympathetic) to the limb form a rather less numerous series* than do the sensory distributed to it, so the series of the latter is again rather less numerous, less extensive, than of those which by excitation approximately minimal will evoke reflexly a movement of the limb. The spinal apparatus of the limb may therefore be likened to a funnel, the wide entrant mouth of which is represented by sensory nerves, the narrow end of exit by the spinal motor roots to the musculature. In the upper limb the sensori-motor funnel has the following segmental extension :—

	Cervical.							Thoracic.				
Number of spinal nerve—	II.	III.	IV.	V.	VI.	VII.	VIII.	I.	II.	III.	IV.	V.
which evokes reflex movement of limb .		+	+	+	+	+	+	+	+	+	+†	
which supplies sense-endings in skin of limb			+	+	+	+	+	+	+	+		
which supplies motor innervation to muscle of limb				+	+	+	+	+	+			

and in the lower limb the following :—

	Thoracic.		Post-thoracic.									
Number of spinal nerve—	XI.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
which evokes reflex movement of limb .		+	+	+	+	+	+	+	+	+	+	
which supplies sense-endings in skin of limb			+	+	+	+	+	+	+	+		
which supplies motor innervation in muscle of limb				+	+	+	+	+	+	+		

By the above it is seen that centripetal impulses entering the spinal cord in the neighbourhood of the limb regions tend to be led into those regions, in other words, irradiation is largely directed into those regions, and this both from above and from below. On the other hand, impulses entering the limb region by roots belonging to the sensory nerves of the limb do not so tend to irradiate beyond the confines of the limb region. Thus, impulses arriving *viâ* the sensory root of IIIrd cervical usually evoke action of supinator longus more readily than impulses arriving by the sensory root of VIth cervical evoke action in any part of the musculature belonging to IIIrd cervical. Again, impulses poured into the sensory root of the Ist post-thoracic usually evoke action of the flexors of the knee more readily than do impulses poured into the sensory root of the VIth post-thoracic evoke contraction of the musculature innervated by the Ist post-thoracic.

I have given above as a broad rule of "reflex spinal spread" that, taken generally, there exists for each afferent root a reflex motor path or arc in its own spinal segment offering as little resistance as any open to it anywhere. Although that is so, there usually exist in each spinal segment certain groups of motor nerve-cells

* SHERRINGTON, 'Phil. Trans.,' B, vol. 184.

† Not always.

which are only with great difficulty reached or excited by excitor impulses conveyed into the segment by the fibres of its own afferent root.

In a spinal segment of the limb region among the entire collection of its motor nerve-cells certain sub-groups are far less excitable in local spinal reflexes than are others. In other words, of the entire contraction produced by direct excitation of a whole motor root certain parts are elicitable by spinal reflex much less easily than other parts. Whereas, between its own afferent root fibres and some of the motor neurons of the segment connection is facile, resistance low, between its afferents and others of its motor neurons connection is difficult, resistance high. Hence, under the conditions maintained in my experiments, the centrifugal discharge, although occurring contemporaneously in several segments, in each of the several segments engaged certain only among the motor neurons. The motor discharge although pluri-segmental is in each segment only fractional: certain neurons in the segment are selected, certain neglected. The nature of the selection recurs with a degree of constancy altogether remarkable, although not invariable.

Examples:—Good contraction of supinator longus group in arm of *Macacus*, by excitation of dorsal (afferent) root Vth cervical nerve with KRONECKER secondary coil at 15 k.s.; to evoke contemporaneous biceps action as well as supinator, secondary had to be brought up to 90 k.s. No contraction of triceps could be provoked contemporaneously with supinator longus.

In the Cat, cerebrum and cerebellum above their crura having been ablated, and the cord transected above IInd cervical nerve, a touch on the roof of the mouth causes wide opening of the mouth, *i.e.*, depression of the mandible. The elevators of the jaw being much more powerful than the depressors, the afferent path (Vth cranial) must have selected the motor neurons of digastric, mylo-hyoid, &c., and neglected comparatively, or absolutely, or inhibited those of the elevator muscles.

The intercostal muscles cannot at all readily be reflexly excited *viâ* the lateral cutaneous branches of the corresponding spinal nerves, but the superficial muscles of the chest can be.

Excitation of the lateral cutaneous branch of the IInd thoracic only with difficulty evokes any pupil reflex, the entire afferent root of IInd thoracic evokes reflex dilatation fairly readily. In the same way lateral cutaneous branch of IInd thoracic evokes retraction of shoulder very easily, but only with difficulty any contraction in the intercostal muscles.

Again, of the muscles of the front of the thigh, some tend to be brought into reflex play by the internal saphenous nerve—playing upon the spinal segments of those muscles *viâ* their own proper afferent roots—much more readily than others; the rectus femoris (its upper part especially), sartorius and fascialis much more readily than the crureus and vasti. Excitation of the central end of the nerve to one of the vasti evokes contraction of its own fellow vastus, and the associated crureus less easily than sartorius and a part of the rectus femoris.

Again, excitation of the central end of the nerve to one head of the gastrocnemius evokes contraction in the hamstring muscles more readily than in the *gastrocnemius itself* and the soleus.

Again, excitation of the plantar nerves evokes contraction more readily in the pre-tibial muscles than in the post-tibial group, though segmentally they belong rather to the post-tibial group than to the pre-tibial.

It can be said, that of the movements of the limb, some are easily provoked by spinal reflex action, some only rarely and with difficulty. Among those induced as primary spinal reflexes (the cord being transected above) are, in order of facility of production in my experience :—

In the *upper limb :*

retraction of upper arm.
flexion-adduction of thumb.
extension of wrist (especially in Cat).
adduction at shoulder.
flexion of elbow.
flexion (less often extension) of digits (always in accompaniment to flexion-adduction of thumb).
slight pronation of forearm (especially in Cat).
abduction at shoulder.
extension of elbow (rare).
less common is flexion and some pronation of wrist.

In the *lower limb :*

flexion of hip.
flexion of hallux.
flexion of knee.
adduction at hip.
flexion (less often extension) of digits (always in accompaniment to flexion-adduction of hallux).
flexion—less commonly plantar flexion—of ankle.
less common is extension of hip.
abduction of hip (not common).
extension of knee (rare).

The preponderance of the above movements over others in the limb is exemplified in the following summary of movements, commonly evoked by excitation of various peripheral nerves in the limbs. The transection of the cord had, in most of the cases on which the summary is based, been made from a few days up to six months prior to the observation.

Internal saphenous nerve in highest third of thigh (Monkey) evoked flexion of hip ; flexion of knee.

Internal saphenous nerve just above knee (Monkey ; cord cut at VIth thoracic level five months previously) evoked flexion of hip, adduction of thigh, slight flexion of knee, movement of tail to the homonymous side.

Internal saphenous nerve at knee (Dog), flexion of hip, with some feeble flexion of knee (Cat) ; flexion of hip, especially due to fascialis and upper part of sartorius of quadriceps, with some flexion of knee, and usually some dorso-flexion at ankle.

Internal saphenous nerve at the ankle (Monkey), flexion of hip, with slight flexion at knee.

External saphenous nerve near ankle evoked flexion of knee, flexion of hallux and toes, depression of tail, sometimes abduction of tail.

The most lateral digital branch from the musculo-cutaneous on the dorsum of the foot evoked flexion of hip, slight action of hamstring muscles, slight dorsal flexion of ankle.

Internal plantar at heel (Monkey) evoked dorso-flexion of ankle, flexion of hallux (less easily flexion of short digits as well), flexion of knee, slight flexion of hip.

Internal plantar at heel (Cat), dorso-flexion of ankle and flexion of knee.

External plantar at heel (Monkey) evoked dorso-flexion of ankle, flexion of hallux and digits, flexion of knee, and some flexion of hip; (Cat) dorso-flexion of ankle, with slighter flexion of knee.

Cutaneous branch of musculo-cutaneous at annular ligament: dorso-flexion of ankle, with some inversion of foot; slight flexion at hip and knee.

Hamstring nerve evokes flexion at knee and hip, with generally crossed extension of knee and ankle, including contraction of extensors of knee and relaxation (inhibition) of the hamstring muscles.

Nerve to outer head of gastrocnemius (Cat) evokes usually contraction in the dorsal flexors of ankle, less usually contraction in gastrocnemius itself, and very usually contraction in the flexors of the knee.

Peroneal nerve at knee (Monkey) evokes flexion of knee and hip, dorsal flexion of ankle, and flexion of digits; abduction of tail.

Peroneal nerve at knee (Cat), flexion of knee, hip, and dorso-flexion of ankle.

Popliteal nerve at knee (Monkey) evokes flexion of knee; tail abduction; adduction of both thighs.

Popliteal nerve at knee (Cat), flexion of hip and knee, generally extension of opposite knee.

Dorsal branch of ulnar on hand evokes flexion of digits, extension of wrist, pronation (slight) of forearm, flexion of elbow, some retraction at shoulder, and extension of opposite elbow.

To these may be added the list of root reflexes, pp. 130–133, above.

It is very obvious from the above that in these spinal reflexes of the limb certain limb movements are of very preponderant occurrence; in other words, certain functional groups of motor neurons are less easily excited than others by the incoming local impulses. SANDERS-EZN,* SCHLOESSER,† and LOMBARD ‡ have pointed out how difficult it is to evoke extension of the knee as a spinal reflex movement. In a previous paper I noted that in the Monkey the representations of movement in the cord, as tested by excitation of the ventral spinal root and of the dorsal (afferent) root, do not coincide; in fact, by no means coincide. SANDERS-EZN,§ LOMBARD,‖ and myself ¶ have pointed out that the movement elicited by excitation of the afferent root is often widely different, or even the converse, of that evoked by excitation of the efferent root corresponding. The list of reflex movements gives many examples. In Monkey, the VIIth post-thoracic afferent root provokes flexion of ankle; the corresponding motor root gives extension at ankle. The VIth post-thoracic afferent root evokes flexion of hip; the corresponding motor root gives extension. The Vth post-thoracic afferent provokes flexion of knee; the corresponding motor extension at knee. In the Cat, VIIIth post-thoracic afferent provokes flexion at hip and dorsal flexion of ankle; the corresponding motor, extension at hip and plantar

* *Loc. cit.*

† 'Archiv f. Physiol.,' 1880.

‡ *Loc. cit.*

§ LUDWIG'S 'Arbeiten,' 1867.

‖ 'Archiv f. Physiol.,' 1885.

¶ 'Journ. of Pysiol.,' vol. 13, p. 621, 1892; (recently P. MAY, 'Phil. Trans.,' B, 1896, C.S. 1897).

flexion at ankle. VIIth post-thoracic afferent elicits flexion at hip and knee; the corresponding motor extension at hip and knee. The VIth post-thoracic afferent root evokes flexion at knee and hip; the motor extension. The Vth post-thoracic afferent, flexion at knee; the corresponding motor extension at knee. In the Monkey, VIIth cervical afferent very frequently evokes flexion at elbow; the VIIth motor root gives, on the contrary, extension of elbow. In the Cat, the same roots also give conversely flexion and extension at wrist. The IInd cervical afferent root evokes turning of the head to the opposite side; the motor root produces lateral flexion of the head to the same side. SANDERS-EZN's phenomenon of the predominance of flexion over extension at knee-joint is well illustrated by the case of two monkeys examined in the laboratory almost daily for three months after transection in the thoracic region. Hardly once in all that time was homonymous extension of the knee elicited from either, although flexion at knee was day after day easily elicited. In the Dog I have sometimes failed to find any motor root or set of motor roots which gives flexion at the knee, extension always predominating; yet flexion at knee is easily obtained in the dog as a reflex from almost any nerve in the whole limb, or by a stimulation of almost any part of the skin of the limb, as was noted by FREUSBERG,* in his well-known account of reflexes obtainable from the lumbo-sacral cord of the dog. Again: the blow on the tendo patellæ which evokes the direct (WESTPHAL,† WALLER‡) spasm of vastus medialis and crureus§ called "knee-jerk," fails to elicit any true reflex contraction of those muscles, although frequently evoking a true reflex contraction of the hamstring muscles, which, as LOMBARD|| has shown, succeeds the direct extensor spasm. That this hamstring contraction is a true reflex can hardly be doubted, in view of the extreme facility with which the hamstrings are reflexly excited, and also in view of a fact I have often seen, that the hamstring contraction evoked by the tendon tap occurs even when the dissected hamstrings, altogether freed at their lower ends, are lying slack, and when their own afferent roots have been cut through.

Again, the movement evoked by a lower sacral or coccygeal afferent root is often an abduction of tail in absolutely the reverse direction of that given by excitation of the corresponding motor root.

The list suffices to illustrate the point, a corollary from the previously given rule; and it emphasizes what I have already insisted on, the negation of the view (OS. POLIMANTI, R. RUSSELL) that in the movement produced by direct excitation of a whole motor spinal root we reproduce a functional movement of high co-ordination.

This inequality of excitability *viâ* local reflex paths, evidenced by the motor neurons

* PFLÜGER's 'Archiv,' vol. 9.

† 'Archiv f. Psych. u. Nervenkrank.,' vol. 5, p. 803.

‡ 'Brain,' vol. 3, p, 179; 'Journ. of Physiol.,' vol. 11, p. 384.

§ SHERRINGTON, 'Journ. of Physiol.,' vol. 13, p. 621.

|| 'Journ. of Physiol.,' vol. 10, p. 122.

of muscles acting antergetically about a joint, is not similarly great for all joints; thus, the inequality between flexors and extensors of knee seems certainly greater than between extensors and flexors of hip, and than the inequality between extensors and flexors of elbow. It is not to be forgotten that this inequality may be less an inequality of accessibility to impulses or influence, than an inequality of distribution of excitor impulses, influence being brought to bear on the other neurons, but in the sense of inhibition, as is certainly the case in some instances (see pp. 177, 178). It is significant that the arrangement is not that all the muscle-groups about one joint are relatively inaccessible, and all the groups at another joint accessible, but that the difference is between antagonistic groups acting about one and the same joint.

Quite in accord with their difference in degree of approachability by local afferent channels of short paths, is the difference of degree of amenability to local play of tonic influence exhibited by various sub-groups of motor neurons. In illustration, I give the following:—The cord having been transected in the lower thoracic region, the Monkey frequently develops, in the course of some weeks, marked rigidity of the lower limbs. Certain muscles become spastic and rigid, and gradually cease to be ever fully relaxed, and structural rigidity may in time supervene. The hypertonic and rigid muscles are especially the flexors of the hips and of the knees. In five months' time, the position permanently assumed by the limbs is as follows: they are drawn up and somewhat crossed. The flexion of hips and knees may be extreme, the adduction of the thighs is less. I cannot myself escape the conviction that the position assumed by the limb, and the late rigidity itself and its distribution in the musculature, is the natural outcome of the fact that after the cord had been sundered from the brain the inequality of incidence of the local stream of centripetal impulses, and the fact that at its *embouchement* it selects, employs, and discharges motor neurons for flexion of hip and knee, and neglects the antergic extensors, leads, in due course, to a permanent upset of balance between the two, in which relative over-action is continuous in the one, and atrophy, yielding and under-action existent in the other. In one Monkey, the amount of rigid flexion of the hips and knees was unequal on the two sides, the left hip and knee being kept more flexed than the right: in this animal, reflexes were more easily elicited from the skin of the left limb than of the right, but owing to the more rigid condition of the left limb, the movement obtained was generally less in the left than right limb. It was, in fact, contrary to a rule given (p. 172), easier to obtain movement of the right hip and knee from many parts of the skin of the left limb than from the skin of right itself. From the front of the left thigh, flexion of the left hip and adduction of the right thigh, with slight extension of the right knee, could be regularly evoked. The greater rigidity was, therefore, present in that limb which possessed the greater sensitiveness. This supports, therefore, the view of the spinal reflex origin of the late rigidity which I here put forward. The same explanation, with little modification, may apply to the later rigidities occurring in limbs, subsequent to lesions of the limb areas of the cortex cerebri. After reading the recent admirable account by HERMANN MUNK,* of rigidities after cerebral ablations in the Monkey, I should quite agree with him that in the constant assumption of the sitting pose in cramped cages, an important adjuvant condition in the production of late rigidity in the Monkey has been discovered by him. At the same time, in the occurrence of late rigidity of the lower limbs after spinal section, I look upon a natural inequality of reflex spinal play in, or employment of, individual spinal mechanisms (*e.g.*, reflex spinal flexion of knee, and reflex spinal extension of knee respectively), and the gradual, almost inevitably resulting loss of functional balance between antergic sets of spino-muscular apparatus as the prime factor. For instance, flexors of the knee become contracted when the cord is transected, because extensors, practically inaccessible to spinal reflexes of short path and of ordinary stimulus-intensity, never exert that normal maximal stretching which, even if artificially given from time to time, successfully defers their surrender to contracture. My view is that the contracture is the expression and result of the over-balance of the spinal tonus of the extensors of hip and knee by that of the flexors. The normal tonus of the skeletal muscles when the nervous system is intact has, doubtless, spinal, cerebellar and cerebral factors, which are in it algebraically summed. In the spinal experiments now under consideration of these several factors, only that of the cord itself is effective, the transection having cut off all the others, and in these contracture experiments necessarily only that of the lower half of the cord. That remnant of the normal tonus I refer to as *spinal* tonus, in contradistinction to the tonus described at p. 174 in this paper, ensuing on ablation of the cerebral hemispheres, which I term *decerebrate tonus,* also in contradistinction to that tonus which I term decerebellate ensuing on removal of the cerebellum. The late rigidity of paraplegia in the Monkey is an expression of the upset of balance of the spinal tonus in antagonistic muscle-groups. I look upon its origin as of reflex† nature, and this is borne out by the fact that in my Monkeys it could, in its earlier stages, *i.e.*, before structural changes in the muscles set in, be set aside by chemical anæsthesia, and by applying an ESMARCH bandage to the limbs. The unequal degree of spinal tonus, *idem aliter* of spinal reflex action is, in my view, of prime importance in the production of late rigidity.

This view appears to me consonant with, although widely removed from, that advanced by H. MUNK. It harmonises with his view, in so far that confinement in a cramped cage might still further reduce the opportunity for extension of the knee or hip, even when that movement occasionally arose. It may be objected that if, as I urge, there is a considerable and constant difference in spinal excitability between the motor spinal centres for flexors and extensors, *e.g.*, at hip and knee, such should

* 'Sitzb. d. Königl. Akad. d. Wiss. zu. Berlin,' 1895.

† 'Proc. Roy. Soc.,' vol. 53, 1893.

be demonstrable; but, as I have shown,* strychnia spasms involve extensors and flexors, *e.g.*, at knee and ankle, synchronously and impartially, although according to doctrine † of reflex spinal origin. It is, of course, well known since SANDERS-EZN ‡ (1867) that the very spinal nerves whose motor roots by direct excitation produce extension of knee when reflexly excited evoke flexion of knee; on the other hand, I am not convinced that in the Mammalian cord strychnia spasms are always of purely reflex nature. The spasms of asphyxia are often certainly not reflex, but direct, and in spite of the excellent experiments of H. E. HERING in the Frog, I have in a number of experiments found the exhibition of strychnia still produce spasms, when the possibility of asphyxial complication has been avoided after all the afferent roots belonging to the whole length of the isolated spinal cord below transection had in the Cat and Dog been cut through, and when it has been proved by subsequent dissection that not a single afferent root filament had been left.§ This result is obtained even when a period of six to seven hours is allowed for subsidence of the current of injury in the severed nerve-fibres of the afferent roots. I think, therefore, these experiments prove that strychnia acting upon a portion of Mammalian spinal cord that has been severed from the brain can excite the motor neurons in it either directly or induces in them some autochthonous excitation. That this mode of excitation does not discriminate between these functional groups of neurons in the same manner as excitation of the posterior roots is interesting but not opposed to the above view. On local reflex action the activity of the flexors at knee and elbow predominate over the extensors. Conversely in strychnia spasm the extensors predominate. In most local spinal reflexes, as I pointed out some time since,‖ only *one* set of an antagonistic muscle-couple contract; in strychnia spasm, when severe, both sets usually contract synchronously.

In the same way, asphyxia, especially when produced rapidly, evokes discharge of the motor neurons of the cord, and the discharge produced by it, is of both extensors and flexors, and occurs as readily when all the afferent roots of the limb have been severed as when the afferent roots remain intact. The chemical excitation of the asphyxial condition so far resembles that of strychnia that in contradiction to the tonic conditions under discussion here, it is due to an excitation not conveyed *viâ* the afferent roots but must be autochthonous in the gray matter of the cord. I do not

* 'Journ. of Physiol.,' vol. 13, 1892.

† Compare lately EWALD HERING, PFLÜGER'S 'Archiv,' 1893.

‡ LUDWIG'S "Arbeiten," 'Sitzungsb. d. Sächs. Ges. d. Wiss.'

§ [In saying the above I do not intend to controvert the likelihood that under ordinary circumstances the convulsions of strychnia-poisoning are largely of reflex origin. H. E. HERING has thoroughly shown that strychnia convulsions are set in abeyance by severance of the afferent nerve-roots. In my experiments large doses were given, and the object of the experiments was to decide whether, in the absence of sensory paths and without the concurrence of asphyxia—which latter of itself can produce autochthonous convulsions—strychnia can still produce spinal convulsions in Mammals; it does. 10th July, 1897.—C.S.S.]

‖ 'Journ. of Physiol.,' vol. 13, p. 621, &c., 1892.

mean to infer that these two modes of chemical excitation act entirely similarly, and, indeed, there is obviously a predilection in the case of strychnia for the motor cells of the somatic muscles, in the case of the asphyxial condition for the visceral muscles (*e.g.*, the arrectores pilorum), or rather for the spinal motor neurons of the sympathetic; I mean, merely, that both stand out together in strong contrast with such a condition as *decerebrate rigidity* following removal of the cerebral hemispheres, for in this last the contraction of the extensors of elbow and knee can be almost immediately reduced or abolished by *severance of the afferent roots* of the spinal region.

Again, extensors of the knee appear more readily excited from the cortex after severence of the lumbo-sacral afferent roots. In our experiments on the influence of the sensory roots of the limbs on the co-ordination of their movement, Dr. MOTT and myself noted* that, in the co-ordination produced, proneness to extension of the knee played a part. Dr. MOTT allows me to mention this, and it will be dealt with more fully in our complete paper, still to be published.

Motor Cells exhibiting in the self-same Segment marked Inequality of Accessibility to local reflex pressor Impulses innervate antergetic Muscles.

Of the functional groups of motor neurons in the cord some, in view of the actions of the muscles they innervate, may be termed *synergetic* with some, *antergetic* to this or that other. Those of the flexors of knee may thus be said to act in synergy with those of the flexors of the hip, but in antergy to those of extensors of knee; also in a certain measure to those of extensors of hip. These last are in synergy with the extensors of the knee, but in antergy to flexors of hip; also in certain measure to those of knee. *The groups of motor neurons which in one and the same spinal segment exhibit marked inequality of local reflex excitability innervate antergetic muscles.* So much is this the case that in reflex movements of local spinal origin, it is the rule for only one set of an antagonistic couple of muscles to be thrown into contraction, and especially for only one group of antagonistic groups to be contracting at the same time. I have already alluded to this, and pointed it out in a previous paper,† but will add here further illustrations.

Flexion of ankle by dorsal flexors, the post-tibial and crural muscles remaining absolutely without contraction, in response to excitation of internal plantar nerve (or external plantar, or cutaneous of musculo-cutaneous generally).

Contraction of those parts of quadriceps extensor (rectus internus and fascialis) which flex the hip, while the part that extends the knee remains absolutely without contraction, in response to excitation of long saphenous nerve. Contraction of flexors of elbow, the triceps‡ remaining quite flaccid.

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* 'Proc. Roy. Soc.,' vol. 57, 1895.

† 'Journ. of Physiol.,' vol. 13, p. 621.

‡ Except for a part which retracts the arm without extending the elbow.

Contraction of the triceps of the arm, while biceps and brachialis remain absolutely without contraction, in response to excitation of the afferent root of the VIIIth cervical nerve.

Contraction of the extensors of the wrist, the flexors remaining absolutely without contraction, in response to touching the fore-pad of the Cat.

Contraction of the flexors of the elbow, the extensors remaining absolutely without contraction, in response to thermal stimulation of the palm (Cat).

Contraction of the adductors (pector. maj. and latiss. dorsi) at shoulder, the abductors remaining quite slack (deltoid).

In dealing with rules of irradiation in spinal reflexes, I have mentioned reasons for believing the groups of motor neurons innervating small pieces of musculature, acting synergetically upon the self-same joint, to be commonly treated by the spinal action as entities, and employed as units in these spinal reflexes. From that and the foregoing it follows that in adjoining spinal segments the groups of motor nerve-cells contemporaneously selected for excitation by spinal reflex action are synergetic, not antergetic. This is, of course, the reverse of what since WINSLOW* and DUCHENNE† has been common belief concerning the co-ordination of "willed" movements of Man, but it agrees with the co-ordination which I have proved to take place in the Frog.‡ I have shown that in the limb, while for muscles antergetic at the distal joints the groups of motor neurons largely overlap each other in segmental position, the groups of muscles antergetic at the proximal joints of the limb do not so largely segmentally overlap. Hence the reflex spinal discrimination between motor neuron-groups for the antagonistic musculature of the proximal limb-joints involves a field wider than merely three adjoining segments.

But not only are certain of the movements about a single joint opposed to each other, certain movements at one joint are opposed to certain movements at neighbouring joints. Thus the extensors of the knee may be called antergetic not only to the flexors of the knee, but also to the flexors of the hip. In such cases the rule above given still holds. The groups of motor neurons selected by the reflex action as it irradiates over spinal segments lying apart in the limb series are still those of synergetic muscles. For instance, while the reflex movement evoked by excitation of the IVth post-thoracic afferent root, or that responsive to the long saphenous nerve, usually primarily contracts the flexors of the hip, it involves next, not the antergetic muscles in the nearest spinal segments (*e.g.*, vasti and crureus), but neglects these and embouches into the synergetic of more distant segments, *e.g.*, the hamstring muscles. *In this way the reflex action, by its "spread," develops a combined movement, synthesizes a harmony.*§ Broadly put, there is elicitable as a pure

* 'An Anatomical Exposition of the Structure of the Human Body.' 4to. London, 1749.

† 'Physiologie des Mouvements.' Paris, 1867.

‡ 'Journ. of Physiol.,' vol. 13, 1892.

§ [It must be remembered, however, that the extensors at some joints are synergetic, not antergetic, to the flexors at other joints; this has been especially shown by H. E. HERING in an article published since this communication was sent to the Society. HERING calls such muscles pseudo-antagonistic to each other. An example of such action, especially studied by him, is the pseudo-antagonism of the extensors of the hand with the flexors of the fingers.—10 July, 1897. C. S. S.]

spinal reflex from the lumbo-sacral region, but one movement of the limb as a whole. This movement is a combined movement of general advance and flexion of the limb. It is combined of flexions of hip, knee, ankle (dorso-flexion), and digits. These components of the combined movement appear in accordance with the rule of segmental proximity to be each rather more readily elicitable *vià* afferent roots of the segmental locality of their own motor neurons than *vià* roots belonging elsewhere. Nevertheless each, when the excitation is pushed, tends to have associated with it more or less of the rest of the general movement of flexion. It is hardly too much to say that there is in this limb-region of the cord of, for instance, the Dog, from the point of approach of the local afferent channels, but one motor centre, and this the one which produces general flexion of the limb. Into it at one point or another lead all and each of the afferent channels which provoke movement of the limb at all; and the outcome is therefore, broadly stated, monotonously flexion. Similarly, with the fore-limb the combined movement of flexion at elbow, extension at wrist, and flexion (*i.e.*, retraction) at shoulder, is *the* movement elicitable from the limb as its local homonymous spinal reflex action. There is, however, it is true, *emphasis* on or predominance of this or that detail, according as this or that particular nerve-root or nerve-trunk affords the particular channel of approach. The arrangement of the intra-spinal resistance is such as to make certain functional groups of the motor neurons especially easy of access to, broadly speaking, all the afferent channels of the limb. Inasmuch as the motor groups thus found to be especially easy of access are such as, when synchronously active, give one harmonious movement of the whole limb—*e.g.*, drawing it upward and forward by co-operative flexion at the various joints—these groups can be considered to constitute one large functionally-connected nucleus, which itself may constitute an entity in the co-ordination of the limb in the movements of the body taken as a whole.* It is conceivable that such a nucleus is dealt with as a whole, especially when the long cerebro-spinal arcs—ruptured in my experiments—remain intact.

Rule of Uniformity of Response despite Spatial Variety of Provocation.

From the above we are led almost as a corollary to a *rule of uniformity of response despite spatial variety of provocation*, for it is obvious that excitation of any one of a large number of afferent channels will evoke approximately the same movement in reflex response.

Examples:—The digital nerves of foot or hand separately excited evoke the same movement, although their segmental value and root composition is severally very different, varying from 5 + 6 to 7 + 6 in

* [This prediction was confirmed in two Notes communicated by me to the Society ("Cataleptoid Reflexes in the Monkey," 'Proceed. of Roy. Soc.,' Dec., 1896. "Reciprocal Innervation of Antagonistic Muscles," Third Note, Dec., 1896), after the present paper had been sent in.—10 July, 1897. C. S. S.]

the foot, and from 6 + 7 (+ 8) to 1 + 8 in the hand. The same result occurs when, instead of the nerve-trunks, various points of the skin of hand and foot are excited.

Again:—If, in the Cat, the cord is divided at XIth thoracic level, and the afferent roots of IIIrd, IVth, Vth, VIth, VIIIth, IXth, and Xth right post-thoracic nerves cut, the field of æsthesia of the right limb is that of the VIIth post-thoracic nerve. The reflex movements elicitable from this field is then studied with special regard to difference of movement in result of difference of locality of stimulation. The field of remaining æsthesia includes whole of foot, the outer and (less) the inner aspect of the ankle, the outer aspect of the lower half of the leg, and the calf nearly up to the popliteal space. A slight pinch of the skin at any point within the whole of this area elicits a contraction in the hamstring muscles and in the median half of the gracilis; this contraction is accompanied by flexion of the ankle, and by some spreading of the toes when the pinch is applied to the dorsum pedis or planta, especially the pad. The contraction in the hamstring muscles is chiefly in the inner hamstrings when the inner side of the foot, chiefly in outer hamstrings when the outer side of the foot, is the place of provocation. A deep reflex, *e.g.*, a pinch of the tibialis anticus tendons, elicits the same contraction of medial half of gracilis as do the skin reflexes. A crossed reflex, exciting the crossed quadriceps extensor cruris, was obtainable from the whole of the skin area.

Again:—If the afferent roots of the limb-region of the Dog are split up into a series of filaments, twenty-five in number, all fairly equal in size (I have prepared the filaments as follows :—IXth post-thoracic, one filament; VIIIth post-thoracic, four filaments; VIIth post-thoracic, six filaments; VIth post-thoracic, five filaments; Vth post-thoracic, three filaments; IVth post-thoracic, two filaments IIIrd post-thoracic, two filaments; IInd post-thoracic, one filament), excitation of each of these, except the first and sometimes the twenty-fifth, usually readily evokes flexion of knee, and from the uppermost twenty flexion of hip can usually be obtained. Sometimes each of the whole series of twenty-five will evoke flexion of knee.

Again:—From the cervical afferent roots of the Monkey, by individual excitation in descending series, contraction of supinator longus muscle is obtainable from each in succession from IIIrd cervical to VIIIth cervical, though not usually inclusive of the latter.

The rule which these examples illustrate may be briefly termed the "*rule of spatial monotony.*" It seems important enough to warrant the subjoined further illustrations, obtained from animals in which there was some depression of spinal reflex activity. The results on the Cat should be compared with the movements obtained from the motor roots of that animal by LANGLEY* and myself.†

CAT: transection above Ist cervical; the movements provoked by exciting the separate afferent roots were—

right	IXth	post-thoracic	root	. .	flexion of right	knee.
,,	VIIIth	,,	,,	. .	,, ,,	knee, hip, ankle, and toes.
,,	VIIth	,,	,,	. .	,, ,,	knee, hip, ankle, and toes.
,,	VIth	,,	,,	. .	,, ,,	knee, hip, ankle, and toes.
,,	Vth	,,	,,	. .	,, ,,	knee, hip.
,,	IVth	,,	,,	. .	,, ,,	hip, knee.
,,	IIIrd	,,	,,	. .	,, ,,	hip.
,,	IInd	,,	,,	. .	,, ,,	hip.

* 'Journ. of Physiol.,' vol. 12, p. 366.

† 'Journ. of Physiol.,' vol. 13, p. 621.

MONKEY: transection above Ist cervical—

right IXth post-thoracic root	. . flexion of	great toe.
,, VIIIth ,, ,,	. . ,,	great toe.
,, VIIth ,, ,,	. . ,,	great toe, knee, and hip.
,, VIth ,, ,,	. . ,,	great toe, knee, and hip.
,, Vth ,, ,,	. . ,,	great toe, knee, and hip.
,, IVth ,, ,,	. . ,,	hip and knee.
,, IIIrd ,, ,,	. . ,,	hip.

Turning of the head and neck away from the side excited is obtained as a bulbo-spinal reflex from stimuli to nostril, lip, back of cheek, pinna, back of neck, or from nerve-roots, *e.g.*, Vth cranial, Ist, IInd, IIIrd, often from IVth and Vth, cervical nerves; this movement is similar to that discovered as a cortical reaction by FERRIER, and studied by SCHÄFER, MUNK, and others. I would call it the *wry-neck* reflex. It is another example of an action usually considered to be peculiarly "cortical" in character, but really pre-eminently represented also in the "lowest level" centres as HUGHLINGS JACKSON terms the bulbo-spinal.

A very striking character of the reflexes elicitable from the isolated Mammalian cord is the machine-like want of variation with which, on repeating the stimulation, the movement is repeated. Of this fatality, temporal monotony, or monotonous repetition, it is not necessary to give further example than the flexion of thumb or hallux that follows uniformly each time the little finger or toe is pinched. It is true that after the first few repetitions (*Bahnung*) a slighter pinch than that required at first generally becomes adequate, or the reply from the same degree of stimulus becomes more extensive, and that after twenty or thirty repetitions an interval may ensue during which the movement becomes less, and may even be scarcely perceptible; then it returns again gradually, recovering, as it were, from fatigue. The *breakdown due to fatigue appears to involve the afferent rather than the efferent apparatus*, at least to affect it *earlier*, for, if *another* finger or toe be excited, the movement is at once elicited from it, in accordance with the rule of spatial monotony. Among the deep reflexes a good example of monotony of repetition is contraction of the median part of the gracilis muscle, which occurs each time one of the two tendons of the tibialis anticus muscle is nipped above the annular ligament (Cat).

THE "MARCH" IN SPINAL REFLEXES OF SHORT PATH.

The reflex movements elicitable from the Mammalian spinal cord after cross-section are often extremely brief—surprisingly so; in fact, as FICK* has pointed out in dealing with the dorsal nerves of the Frog, often like simple motor twitches. The

* PFLÜGER'S 'Archiv,' vol. 3. See also ERLENMEYER and WUNDT.

movements have seemed to me most brief when least vigorous and most limited in extent, more so in the Monkey in its early condition subsequent to cord-section than in the Cat and Dog under similar conditions. Stimuli that at first elicit only a single movement of a single joint later elicit frequently a short sequence of movements about a series of joints; the capacity for developing a sequence is much earlier regained by the isolated cord of Cat or Dog than by that of Monkey.

For the sequence of movements in a spinal reflex the term which HUGHLINGS JACKSON's writings on epilepsy introduced and have rendered classical will here be used—"*the march.*" As instances of "the march" in spinal reflex movements may be given the following:—

Excitation of afferent root of VIIIth post-thoracic (Monkey) gave flexion of hallux, with some adduction of it, followed by plantar flexion of ankle, followed by movement of tail.

Pinching the back of the thigh towards its medial side high up elicited (Monkey) flexion and adduction of hallux, followed by flexion of knee, followed by movement of tail, accompanied by protrusion of anus.

Touching the skin at the side of the vaginal orifice (Monkey) evoked depression of tail, accompanied by protrusion of anus, followed by flexion of knee, with some abduction of thigh, followed by flexion of hallux.

A long-continued pinch of the pad will in the Cat sometimes induce a short series of alternating flexions and extensions of both hind-limbs, or simply a series of alternating flexions of the two ankles. In the Rabbit similarly a series of flexions of the ankles are sometimes elicitable, but—in accordance with the hopping progression of the animal—are not alternately, but bilaterally, symmetrical. These reflexes can sometimes be evoked by merely holding the animal up so that the paralytic hind-limbs hang.

Touching the pad of the fore-paw evokes (Cat) flexion of all digits, then extension of wrist and pronation of forearm, then flexion of elbow, and retraction of shoulder.

Pinching the outer edge of the sole (*Macacus*) evoked adduction and flexion of the hallux, accompanied by extension of the other digits at metatarso-phalangeal joints, followed by eversion of foot, with dorso-flexion at ankle, followed by flexion at knee and hip, accompanied by adduction toward opposite thigh, and, finally, slight depression of tail and adduction of opposite thigh itself.

Pinching the inner edge of the sole (*Macacus*) evoked adduction flexion of hallux, accompanied by extension of the other digits at metatarso-phalangeal joints, followed by inversion of foot, followed by flexion of knee, in which the inner hamstrings were chiefly concerned.

Pressure close in front of heel (*Macacus*) gave flexion of hallux and other digits, followed by plantar flexion of ankle, followed by flexion at knee. In one Monkey, stroking or blowing upon the hair of one flank evoked flexion of hip, followed by flexion of knee, followed by flexion of ankle and digits.

From a spot in the perineum the following sequence was obtainable; protrusion of anus, followed at once by elevation of tail, succeeded by lateral wagging of tail, continued for about 30 seconds; evacuation of fæces sometimes followed (*Macacus*).

In the Monkey after spinal transection it is quite rare for a moderate stimulus to provoke discharge of successive opposite movements at one and the same joint, *e.g.*, those of lateral wagging of tail or alternating flexions and extensions of limb joints. This is consonant with the rule that the groups of motor neurons most readily combined in action by spinal reflexes are those which are synergetic, not antergetic.

In Cats and Dogs, in whom the depression of spinal reflex action is not so severe as in *Macacus*, the spinal reflexes in their march do combine and discharge, especially in the hind-limbs—where depression is less than in fore-limbs—antergetic groups of neurons in the course of their march, but not (my own experience is never) contemporaneously, though often successively. Hence the *alternating discharges*, which though very rare in *Macacus*, are common and characteristic of the reflexes of the hind-limbs and tail of Cat and Dog, and of the Guinea-pig and Rabbit. In these alternating discharges only one group of an antagonistic couple is discharged at a time. These alternating discharges are especially prone to appear when the stimulation is prolonged. An excellent illustration of this is given by Cat or Dog when one of the hind-paws is pressed between finger and thumb, and continued to be held even after the flexion of ankle, knee, and hip which results; alternating extensions and flexions of the limb then occur, giving exactly an appearance of the limb struggling to get itself free. FREUSBERG'S* "beating-time" reflex (Dog), which can also be studied in the Cat, is another example. The "tail-wagging" reflex, even in isolated tail cord, which I have seen also in the Monkey, is another. The flicking backwards and forwards of the ear in the Cat is another. I would distinguish carefully between these reflexes with "alternating discharge" in antagonistic muscles and the discharge which is merely clonic in character.

It is true that the spinal "march" is much more restricted both in time and place in the Monkey than in other lower laboratory animals. This is an indication of the extent of the shock and of isolation-alteration, both greater in Monkey than in the other types. Yet in a Monkey after complete spinal transection in *the VIIIth post-thoracic segment I have seen, fourteen days after the transection, alternating side to side movements of the tail evoked by excitation of the skin near the tip* of the tail. I have never seen freer wagging of the tail, even when the cord was transected at high thoracic levels. The centre must have lain at the extreme apex of the cauda equina.

No better example could be of the *slightness of solidarity possessed by the isolated cord of the Monkey as a whole*: the reactions obtainable from one local region are not notably increased or more facile when in addition to that spinal region a large part of the adjoining cord remains attached to it than when it is isolated and remains by itself apart from all other regions of the cord. The individual regions of the Mammalian cord, *e.g.*, the limb regions, seem to contain comparatively few parts in their mechanism which are intimately dependent on elements in other regions of the cord outside their own.

It is noteworthy that in the Monkey it is usual for some movements, *e.g.*, the flexion of elbow and flexion of knee, to be, although feeble and difficult to elicit, curiously prolonged and deliberate, the new position assumed by the limb only slowly being relinquished. This character is even better seen, and sometimes is developed

* PFLÜGER'S 'Archiv,' vol. 9.

to extraordinary degree, when the transection instead of being post-bulbar in position is pre-pontine.

The above examples served to show that the rule of segmental proximity operates potently in determining the starting place of the march, *i.e.*, determines the *locus* of the initial and leading movement. Also, that in its progress the march of a spinal reflex, even along short paths, does not exclusively observe PFLÜGER's 4th law, but travels down as well as up the cord. Also, that of two movements evoked which, segmentally considered, are distant, and in the same direction from the starting point, the appearance of the more distant movement rarely precedes that of the less distant, provided the two be in the same lateral half of the body. The upward and downward spread suggests a relation to the intraspinal bifurcation of the afferent root-fibres discovered by FRITHJOF NANSEN (1887),* and confirmed by CAJAL (1889).†

The nerve-cells for the extensors of the knee, rarely as they initiate, *i.e.*, are *primary*, in any spinal reflex, are frequently involved in the later progress of the march. Thus flexion of the knee, combined with flexion of hip and ankle, is frequently followed by and gives way to, extension of knee, hip and ankle; extension at hip is perhaps the most frequent of these extensions. It is noteworthy that in Cat, as I previously pointed out in Frog,‡ the extension is rapid in onset, short in duration, and rapid in disappearance—a kick in fact—as compared with the contraction in the flexors.

For instance, following flexion of the knee, extension frequently occurs in the march of the spinal reflex, started from a pinch of the idio-lateral foot; similarly, it may rapidly follow extension of the hip; or, as a crossed reflex, it may follow and accompany flexion of hip and knee of the opposite side, and in this last case may initiate an alternating "extension-flexion" reflex in the limb of its own side. The relation between the neurons of extensors and flexors at elbow is much the same as between those of extensors and flexors at knee, the flexors of elbow corresponding with flexors at knee. But the difference between flexors and extensors at elbow does not seem to be quite so pronounced as between flexors and extensors at knee. In its behaviour in spinal reflexes, the brachial triceps resembles the extensors of the knee, also in its crossed relation with the flexors of the opposite elbow. In the Cat, contraction of the triceps brachii, as a primary idiolateral local reflex, is rare, but it is quite usually occurrent as the primary contraction of the *crossed* fore-limb, while contraction of the flexors of elbow is the primary contraction in the homonymous fore-limb. But I have seen flexion of the opposite elbow occur on rare occasion in response to strong excitation of the fore-paw of one side in the Cat.

* "The Structure and Combinations of the Nervous System of Amphioxus," 'Bergen's Museum Arsbereting' for 1886. Bergen, 1887.

† "Contribucion al Estudio de la Estructura de la Médula espinal." 'Revista trimestral de Histologia normal y patologica.' March, 1889.

‡ "Lumbo-sacral Plexus," 'Journ. of Physiol.,' 13, 1892.

In the Rabbit, extension of the knee is still rarer as the primary movement of a spinal reflex than even in Cat and Dog, but, on account of the relatively slight depression caused by spinal transection in the Rabbit, it is a very frequent movement in the course of the "march" of a spinal reflex. It does not, however, occur nearly so frequently—in fact, I have never yet seen it occur as the initial movement of the crossed side in the Rabbit—for in Rabbit, flexion of the knee and hip seem the primary crossed just as they are the primary idio-lateral reflexes. This is in obvious relation to the mode of progression of the animal. Thus, in Rabbit, a pinch of the tail will cause symmetrically bilateral flexions, followed by extensions of the hind-limbs, although in the fore-limbs flexion of one fore-limb occurs with extension of the opposite fore-limb. Pinch of one foot will evoke *flexion* of the knees and hips of both sides, instead of flexion of idio-lateral and extension of contra-lateral knee, as is usual in the Cat.

Long Intraspinal Paths.

Throughout the course of the above, I have refrained as far as might be from reference to reflexes of long intraspinal path. The functional regions of the cord may, for convenience, be considered right and left of (1) neck, (2) fore-limb, (3) trunk, (4) hind-limb, and (5) tail (see p. 145). By a "long intraspinal path," I mean one which connects together any two of the said regions without involving cerebellum or cerebrum.

Examples of reflexes, involving long intraspinal paths, are :—

Cat :—Spinal transection above IInd cervical level : compressing left fore-paw between fingers evoked extension of wrist and flexion of elbow, succeeded by extension of left hip with some abduction of it, and usually some flexion of left toes. No movement elsewhere.

Cat :—Transection as above.

Stimulation of either fore-pad evoked lateral abduction of tail, generally toward the side of the foot excited ; no movement elsewhere, except in fore limb excited.

Cat :—Transection as above.

Stimulation of either fore-pad, by touching with a wire, evoked, in addition to movement in same fore-limb, flexion in hip of same side, quickly followed by extension of both hips, with some abduction of both hips.

Cat :—Transection above Ist cervical.

Pinching pinna with fine forceps, near the tip, evokes movement in the fore-limb of the same side. The stimulus is more effective near the tip than elsewhere, and is ineffective along the front and root of the pinna (owing to section). Stimulation of pinna is competent, even when IInd and IIIrd cervical nerves have been severed. Excitation of the central ends of Ist, IInd, or IIIrd cervical nerves has an effect equivalent to pinna. The movement provoked is sometimes flexion, but more usually is extension of wrist and flexion of elbow, with some pronation of forearm ; or extension and flexion may alternate for a short time in a clonic manner. No movement in the other limbs.

Cat :—Cord cut above Ist cervical.

Mechanical or thermal excitation of pinna of either ear evokes clonic flexion of hip, knee, ankle (dorsal flexion), and toes of the same side. No movement in any other limb nor in the tail, but a retraction of the abdominal muscles which appears to be bilateral.

Cat :—Cord cut as above.

Mechanical or thermal excitation of pinna evokes a clonic abduction and extension of both hips earlier and stronger on the same side as the pinna excited, and accompanied on that side only by flexion of the pedal digits.

Cat :—Cord cut as above.

Excitation of pinna evokes following sequence of movements :—

1. Extension of elbow and of wrist in the fore-limb of the same side as the excitation.
2. Flick of tail generally to same side as the side of excitation.
3. Extension of hip, knee, and ankle of same side as excitation, often clonic.
4. Extension of hip, knee, and ankle of opposite side to that of excitation, feebler, often clonic. No movement in opposite fore-limb.

Dog :—Cerebrum and cerebellum removed. Touching nostril evokes turning of the neck and head to the opposite side.

Cat :—Cord cut half way up the bulb; touching the pinna causes the head and neck to be turned toward the opposite side.

Cat :—Cord cut above Ist cervical. Stimulation of either IInd cervical nerve, just beyond ganglion, evokes extension of wrist and forearm of same side as nerve excited, and flexion of hip, knee, ankle, and toes of same side, latter succeeded by extensor sweep of hip and ankle (a kick), and then returning to flexion again. The opposite hind-limb sometimes follows the idio-lateral one, executing a similar movement, alternately with it. The fore-limb movement is tonic, the hind-limb movement is clonic. The movement did not spread to opposite fore-limb.

Cat :—Cord cut as above.

Weak faradic excitation of the central end of the small dorsal branch of the ulnar nerve on the hand produced extension of wrist, flexion of elbow, adduction forwards of arm, so as to turn paw across chest; and evoked, a moment later, abduction and extension of hip of same side and some extension (plantar) of same-side ankle.

Dog :—Cord cut as above.

Excitation of either fore-paw evokes abduction and extension of hip and ankle of same side, quickly succeeded by similar movement of opposite hind-limb. The same spread is not infrequently seen in the Cat, but more frequent is flexion of knee and extension of hip with clonic flexion of the digits.

Cat :—Cord cut above Ist cervical root.

Excitation of either pinna evokes bilateral extension of wrists and elbows, the movement of the same side limb coming earlier and being stronger than that of opposite.

Cat :—Cord cut above IInd cervical root.

Excitation near xiphoid cartilage evokes bilateral extension of hips and ankles, more forcible and earlier in appearance on the side excited than on the crossed.

Cat :—Cord cut above IInd cervical root.

Excitation of skin of perineum provokes, besides movement of tail, an alternating progression movement of both hind-limbs, flexion of right hip alternating with extension of it, and coinciding in time with extension of left. Instead of this alternate movement of the hind-limbs, a synchronous bilateral extension of both hips and ankles, preceded by slight flexion of knees and similar to that got from abdomen is not uncommon.

Dipping fore-paw into warm water causes extension of wrist, flexion of elbow, then slight flexion of knee, and finally extension of hip and ankle.

Dipping hind-paw causes slight flexion at knee, preceding forcible extension of hip.

Dipping end of tail causes wagging of it.

The above are reactions of frequent occurrence. The direction of their spread is not in accordance with PFLÜGER's law,* but is aboral. Thus, excitation started at fore-foot spreads to hind-foot and tail, but not upward to neck; excitation started in neck and pinna spreads to fore-limb, hind-limb and tail; started in hind-limb, spreads to tail, but not to fore-limb or neck. This is true for Cat, Dog and Monkey. The greater facility of spinal conduction in descending than ascending direction is regular and overwhelming in experiments carried out in the above-mentioned way, but yet a certain amount of long, upward spread is observable. Excitation of hind-pad in Cat occasionally evokes, besides movement in its own and opposite hind-limb, a feeble movement in the fore-limb of the same side; this movement is, in my experience, always extension of wrist and elbow with slight retraction of shoulder. The same spread occasionally occurs on increasing excitation applied to VIth post-thoracic afferent root. Spread upward is to the limb of the same side, never in my experience of spinal reflexes is it to the crossed fore-limb and not to the same side fore-limb, and never to either fore-limb without crossing to the opposite hind-limb. LUCHSINGER's† long diagonal spinal reflex between the limbs (in the Newt), I have never met in my experiments with Cat and Monkey. It is noteworthy that extension of elbow and knee, as uncrossed reflexes, are commoner by long spinal arcs than for short.

The fourth of PFLÜGER's‡ classical laws of spinal reflexion states that, with associated spinal reflex centres, spread is always easier from lower to higher, *i.e.*, from more aboral to less aboral centres, than *vice versâ*. H. MUNK§ has expressed the opinion that impulses for touch irradiate easier in a direction from hind-limb to fore-limb, while impulses for common sensation easier in a direction from fore-limb to hind-limb. My own experience is consentient in traversing this fourth law of PFLÜGER. It is well, therefore, while recording the fact, to note that after high transection of the cord, reflexes from the fore-limbs are usually not on the whole so freely evoked as from the hind-limbs and tail. It has often seemed that the motor neurons high up, and therefore nearer the transection, are less receptive of impulses, and are partially blocked or under "shock," especially for impulses arriving at them from sources outside their own local region. Observations on the knee-jerk indicate‖ that, in the neighbourhood of a spinal transection, the short local reflex path and

* 'Über die sensorische Functionen des Rückenmarkes,' Berlin, 1853.

† PFLÜGER's 'Archiv,' vol. 22, p. 179, 1880.

‡ *loc. cit.*

§ 'Sitzungsberichte d. Kön. Akad. der Wissensch. z. Berlin,' 1893.

‖ SHERRINGTON, 'Proc. Roy. Soc.,' vol. 52, 1892.

neuron may, although peculiarly free for and responsive to changes occurring in that short local path, be all the less open to and receptive for impulses approaching by other channels more distant and less local. The local reflex arc might, so to say, be so preoccupied in the business of its own local, and no doubt primary circuit, as to be deaf to reverberations of explosive changes at a distance. Excitation of skin of neck or pinna frequently spreads down the cord and produces movement in tail, or in hind-limbs without evoking a twitch in either fore-limb ; but, as stated above, fore-limb itself can easily be provoked to movement by excitation at the same source on other occasions. That is to say, the downward impulses not unfrequently skip the motor neurons of arm to go to those further down. A point emphasized by the experiments is, that in the chain of spinal centres, the long paths of association connecting different levels are primarily *uncrossed.*

This appears to hold not only for the numerous instances of descendant direction, but also for the scanty ones of ascendant direction. Crossed conduction, on the other hand, seems to exist mainly between segments of not widely different segmental level. Noteworthy is the observation that extension at hip, knee, and ankle is generally characteristic of the crossed reflex ; also that, when a movement is evoked in both hind-limbs by unilateral excitation applied at a distance, *e.g.*, at one pinna, the movement is usually the same in kind in both hind-limbs, *e.g.*, flexion of digits of both feet, extension of both hips, flexion of both knees, but is always the more extensive and powerful in the idio-lateral limb. Similarly, in the case of the fore-limbs, the bilateral movement evoked in them by excitation at a distance, *i.e.*, in some other spinal region, tends to be of symmetrical character, *i.e.*, extension of both elbows, &c.

A remarkable phenomenon of constant occurrence, which illustrates the tendency of impulses to keep to the same side of the cord for considerable distances, is one which may for that reason be introduced here, although its explanation is not easy, and can only be offered after further experimentation. Application of fine electrodes to, or the stabbing with a minute needle of, GOLL's column at the extreme top of the cervical region, and also lower down, evokes movement in the hind-limb of the same side : this movement is nearly always in *Macacus* flexion of digits, in the Cat often flexion of knee. Movement of the thumb and fingers of the hand can be evoked by similar excitation of BURDACH's column, always the hand on the same side only as the column excited. The movement is still perfectly obtained after transection of the cord just above the point of excitation. It is cut out by transection of posterior column alone at various levels below the site of excitation. Anal movements are freely obtainable in this way from column of GOLL at the very top of the cord. The lateral columns of the cord curiously enough do not seem necessary to these movements, and I obtained them in one instance in which I had a pyramidal tract on one side hugely degenerated after ablation (in Monkey) of the whole Rolandic region. Yet the movements were at least as well obtained from the left (degenerated) side as from the right. A phenomenon that may be mentioned in this connection as also employing uncrossed long paths, although not purely spinal, is movement obtainable in the same side fore-limb and hind-limb by faradizing the side of the superior worm of cerebellum. In this case, differently from many spinal reflexes, both sets in antagonistic muscles are usually employed (one relaxing, other contracting—"reciprocal innervation").* I shall refer to this later in this paper. Its resemblance to the previous phenomenon may be but superficial.

In my experience irradiation, "*spread*," *is easier down the cord* from fore-limb to hind-limb than across the cord from fore-limb to fore-limb. On the other hand, from hind-limb spread seems always easier across the cord to the opposite hind-limb than up to the fore-limb even of the same side.

SPINAL CROSS REFLEXES.

By "crossed reflex" is understood a reflex involving travel of nervous impulses across the median plane of the cord. The need for the definition will be obvious in what follows.

The 2nd of PFLÜGER'S† "laws" of spinal reflexion—that termed the "law of symmetry of bilateral reflexes"—states that if to idio-lateral movement there be added, in the course of a spinal reflex, contra-lateral, the latter is symmetrical with the former. The Cat and Monkey afford several examples of this.

Bilateral adduction of thighs (*Macacus*).

Bilateral extension of hips, on stimulation of skin of abdomen (Cat).

Bilateral abduction of hips, with some extension.

Stimulus to fore-limb of Cat; very similar extension and abduction of thighs by stimulating IInd cervical root.

Bilateral protrusion of anus by stimulating one side of the perineum.

Bilateral extension of elbows and retraction of shoulders by stimulating pinna (Cat).

Bilateral flexion of elbows with some supination of both forearms and a forward adduction of both fore-limbs, so that the paws cross each other in front of the chest, from stimulation of one fore-pad embrace reflex.

Bilateral retraction of abdomen on stimulating the side of the chest or upper part of abdomen.

Bilateral flexion of hips and knees on excitation of skin above an ischial tuberosity, in the Cat.

Bilateral protraction of "whiskers" on excitation of skin of the face.

But there are many and important instances which do not conform to the "law." A most important crossed reflex of progression elicitable from hind-limb of Cat and Dog does not conform to it. Under deep, but not very profound anæsthesia, it is a common thing in these animals for alternating flexion of the two hind-limbs to take place. In the Rabbit the flexion of the two hind-limbs, which occurs under similar conditions, is synchronous, not alternate. After spinal transection at the top of the lumbar region the same alternating flexion and extension often is started by

* SHERRINGTON, 'Proc. Roy. Soc.,' 1893.

† 'Ueber d. Sensorische Funct. d. Rückenm.' Berlin, 1853.

merely lifting the animal so that the hind-quarters hang. If, when the movement thus started has ceased and the limbs hang inactive, one hind-paw is pressed, the leg is drawn up, and if the pressure be discontinued, or if the reflex activity is slight, the limb is let down again slowly. If the pressure be, however, continued or the reflex activity brisk, the drawing up of the limb is succeeded by movement of the opposite limb; this crossed movement is usually extension of the knee, generally accompanied by extension of ankle (plantar-flexion), and slight extension at hip. That is to say, the flexors of the knee, so inaccessible, as stated above (pp. 154–156), to the local idio-lateral excitation are delicately sensitive to contra-lateral. The same result often follows electric excitation of either of the plantar nerves, of the cutaneous division of musculo-cutaneous nerve, and of the popliteal and hamstring nerves themselves, *i.e.*, idio-lateral flexion of knee, contra-lateral extension of knee. Sometimes bilateral flexion is obtained, and in the Rabbit, in my experience, crossed flexion instead of crossed extension is the rule.

Again, excitation of VIth and of VIIth post-thoracic roots evokes flexion of idio-lateral knee, hip, and ankle, but extension of contra-lateral knee. Excitation of the perineal skin I have seen give the same. In this reflex there is produced on the crossed side not only excitation of the extensor muscles but *inhibition* of their antagonists. In Dog and Cat, when the flexion of one hip and knee, *e.g.*, right, has been evoked and is in progress, contra-lateral excitation appropriately timed often relaxes the contracted flexors of the right limb. Similarly when after ablation of the hemispheres (Cat, Rabbit), the extensor tonus, which I termed above, p. 159, *decerebrate rigidity*, has set in, excitation of the hind-foot of one side inhibits the contraction of the same side extensors of knee, but increases the contraction of the extensors of the opposite knee. And in the same way, at elbow, the triceps of the crossed side is increased in its contraction, while triceps of the same side elbow is inhibited even to the extent of reaching its post-mortem length. Graphic records show that with the contraction of triceps occurs active relaxation of biceps, with the contraction of biceps occurs active relaxation of triceps, and similarly with the antagonistic muscles of the knee-joint. Similarly excitation of the side of the superior vermis or of funiculus cuneatus (*e.g.*, at calamus scriptorius) causes, during the state of decerebrate rigidity, relaxation of the same side triceps brachii with contraction of the same side flexors of elbow, and at the same time still further relaxation in the opposite biceps and increase of contraction in the opposite triceps. The case of the antagonistic muscles at knee-joint I have similarly examined from sup. vermis and f. gracilis with similar result, except in Rabbit where flexion of both knees seems the rule.

In a Monkey with mid-thoracic spinal transection in the course of months flexion of hip as a crossed reflex developed. It was much easier to obtain this in one limb than in the other, and was obtained more readily as an idio-lateral reflex on that side on which it was the easier as a contra-lateral reflex. Late rigidity affects in the Monkey flexors of hip; I do not therefore lay stress on this instance, but it deserves mention.

The asymmetry of the crossed reflexes of the legs is important because obviously connected with the co-ordination of progression.

The idio-lateral flexion reflex is *prepotent and inhibits* the crossed extension, *e.g.*, stimulation of both feet together causes drawing up of both, so also at elbows. Semisection above the lesion makes the crossed reflex more easily evoked from the side of the semisection. Splitting lengthwise, from top of Vth lumbar to bottom of VIIth, destroys the crossed, but not the idio-lateral. Again, contra-lateral flexion is apt to accompany idio-lateral flexion when the stimulation is strong.

In the Monkey the idio-lateral flexion of hallux knee and hip excited by an excitation of the foot is often followed in the opposite hind-limb by adduction of thigh. In the same animal dorso-flexion of the ankle elicited from the VIIth (afferent) post-thoracic root is often followed by plantar flexion of the contra-lateral ankle. Similarly, in the Cat, when IIIrd, IVth, Vth, VIth, VIIIth, IXth and Xth post-thoracic afferent roots have been severed after spinal transection at XIth thoracic level, a pinch on sole or dorsum pedis, or lateral aspect of lower region of leg and calf evokes idio-lateral flexion of toes, ankle, and knee with some contraction in the idio-lateral gracilis, but contra-lateral plantar flexion of ankle. Again, the reflex, that I call the *torticollis reflex*, breaks this "2nd law" of PFLÜGER, because it employs muscles on both sides of the median plane, and the muscles on the crossed side are not symmetrical with those on the uncrossed.

PFLÜGER'S 3rd law* states that if a spinal reflex is bilateral, the movements on the side opposite to that stimulated is much weaker than the idio-lateral. This is the so-called law of unequal intensity of bilateral reflexes. The experiments in Cat, Dog, and Monkey afford instances of it.

When from one fore-paw bilateral movement of the fore-limbs is excited the movement is less forcible on the crossed side, and also less ample.

When excitation of one pinna evokes bilateral movement in the hind-limbs as described above, the crossed movement is the weaker.

When bilateral retraction of abdomen is excited from the chest wall the crossed retraction is much the less extreme.

In the above described asymmetrical progression reflex the crossed movement is much the less vigorous.

In the bilateral "whisker reflex" the crossed movement is the less ample.

But some reflexes controvert the law.

Both in the Monkey and in the Cat and Dog a touch on the side of the tail at its root usually evokes abduction from the median line and away from the side stimulated. This recalls LUCHSINGER'S reflex from the tail of the Newt. The same crossed action is obtainable, as stated in the list of root-reflexes, p. 130, from the dorsal (afferent) roots of coccygeal nerves. Again a pinch of little toe or a pin-prick at the inner edge of the ischial callosity in Monkey often elicits a similar switch of the

* *Loc. cit.*

tail *from* the idio-lateral side. This reflex not only breaks the 3rd law, but also 1st law, which lays down that if a movement caused by a spinal reflex is unilateral it occurs always on the same side as the application of the stimulus. Caudal lateral movement of reflex spinal origin is however not always abduction from the side stimulated.

Conduction across the median sagittal plane of the cord is certainly very unequally facile at different spinal levels. I have found it curiously difficult to drive irradiation across in the thoracic region from a thoracic afferent root so as to elicit bilateral action of intercostal muscles. It is easier in Cat, Dog, and Monkey to obtain cross-reflex from one hind-limb to the other than from one fore-limb to the other. It is easier to obtain in these species cross reflex from one hind-limb to the other than from a hind-limb up to a fore-limb. It is, however, easier to obtain a reflex from fore-limb to idio-lateral hind-limb than from fore-limb to fore-limb. In the hind-limb of Cat and Dog, the extensor neurons of knee, hip, and ankle have more facile communication with the crossed side of the cord than have the flexor neurons, but this does not seem the case with the hind limb of the Rabbit.

Reflexes elicited by Blows.

A tap on the ischial callosity (tuber ischii) in the Monkey elicits excellently a bilateral adduction of the thighs.

A tap upon the spinal column (skin removed) at the level of the iliac crests evokes rotation outward of both thighs with slight extension of both knees. This must be similar to a reflex mentioned by STERNBERG* as of clinical importance: it involves action of the *glutæi.*

A tap upon the articular surface of the lower end of femur evokes contraction in the adductors of both thighs: the contraction is bilaterally symmetrical, or more often greater on the contra-lateral side.

A tap on lower end of femur, or on insertion of tendo patellæ usually excites dorso-flexion of ankle with slight inversion of foot. This seems to be "ERB's *tibialis anticus* reflex" of clinicians; in my experiments *extensor longus digitorum* replies more amply than does *tibialis anticus.* The tap generally elicits dorso-flexion of the contra-lateral as well as of the idio-lateral ankle.

I am not inclined to consider any of the above to be true cross-reflexes. The so-called *cross knee-jerk* and perhaps the *cross adductor* reflex are not cross-reflexes. That they are reflexes seems certain from the length of their latent period estimated by the time-measurements of BURCKHARDT,† recently repeated with a similar result by GOTCH.‡ The former is contra-lateral and reflex, but not a cross-reflex, for I

* 'Die Sehnenreflexe,' Vienna, 1893.

† 'Ueber Sehnenreflexe,' Bern, 1877.

‡ 'Journ. of Physiol.,' vol. 20.

find it persist *after complete longitudinal splitting of the cord* from a lumbar transection above to the coccygeal nerves below. It must be excited by jar as suggested by WALLER and PREVOST.* And other "jar" reflexes are flexion of hip, protrusion of anus, protrusion of vaginal orifice, all readily excited by a tap on an unyielding part. All the "jar"-reflexes implicate parts easily moved by reflex action, and are cut out by section of the appropriate sensory roots on their own side, *i.e.*, the contra-lateral to application of blow, and not by section of the sensory roots on the side of the blow given. At first sight, inasmuch as they are bilaterally symmetrical, they appear as cross-reflexes, which support PFLÜGER'S "Law of Reflex Symmetry." I would apply WALLER and PREVOST'S explanation of excitation by transmission of mechanical vibration to them as to the so-called cross knee-jerk. I would differ from WALLER and PREVOST, however, in so far that if I understood their meaning aright, they consider the vibration acts as a direct stimulus to the muscle or its motor nerve. I think, on the other hand, the jar excites the afferent nerve-fibres of the nerve-roots corresponding with the muscles, and excites them at or just peripheral to the ganglion. It is remarkable how distinctly, even a slight tap upon the end of one femur is felt by holding the lower end of the other femur, particularly in some positions of the thigh, especially, I think, when the thighs are somewhat abducted.

Some Features of the Muscular Contractions Occurring in Spinal Reflexes.

When spinal depression is great and the reflex movements difficult to evoke they are usually characterised by the following features:—feebleness, restriction of scope, minute tremor, and brevity of duration. As they improve they become more ample, more vigorous, less tremulant or quite steady, and of longer duration. Many of them when quite vigorous are nevertheless clonic; for instance, the abduction of thighs with flexion of toes obtainable in the hind-limb by exciting the fore-paw is in the Cat nearly always clonic. Some are long, *i.e.*, persist for nearly a minute—exhibiting steady contraction all along with a final access (p. 140). This I have seen especially in flexion of knee and in flexion of elbow. Finally, as the reflexes become more active, "march" develops, taking courses as above described. A feature frequent in thoroughly active spinal reflexes is *alternating discharge of antagonistic muscles*, especially, perhaps, at ankle and at wrist. The alternations may recur many times over. The reflex contractions of one of the alternating groups are usually much shorter than of the other: thus, at ankle and wrist the plantar flexion and the dorsal extension are shorter, sharper than the return movements. This I saw in reflexes moving the ankle of Frog, and recorded in a former paper.† WUNDT‡ and FICK§

* 'Revue Médicale de la Suisse Romande,' 1881.

† 'Journ. of Physiol.,' vol. 13, p. 621, 1892.

‡ 'Mechanik der Nerven u. Nervencentren,' Stuttgardt, 1876.

§ 'PFLÜGER'S Archiv,' vol. 3, p. 326.

have noted that some reflex contractions seem from duration and other characters to be simple twitches. In the "tail-wagging reflex" the alternate opposed contractions seem to be about equal in all respects one to the other.

Inhibition in Spinal Reflexes.

It has been shown by GOLTZ and FREUSBERG* that in the Dog spinal reflexes can be inhibited by appropriately timed strong excitations of the skin. Thus, pinching of the tail stops the "beating time" reflex of the Dog. They found, too, that a cord tied round a leg may, in the Dog as in the Frog, make all reflexes inelicitable from the limb for a time. Nipping the tail sometimes succeeds in interrupting micturition in the Monkey—spinal transection in mid-thoracic region. The local homonymous leg reflex will inhibit the crossed (p. 174).

My own observations lead me to believe that *inhibito-motor* spinal reflexes occur *quite habitually and concurrently* with many of the excito-motor described in this paper. In graphic records of the reflex limb movements of the Frog the sudden and absolute relaxation of the muscles of one group at the very moment (to a ·05″) of the onset of contraction in the antergetic group† suggests this. Again, after spinal transection in Dog or Cat the flexion reflex being obtained in the idio-lateral limb by pressing the foot, if while that limb is drawn up by the reflex the other foot is squeezed, not only is the squeezed leg drawn up, but the limb previously flexed is, very usually, let down, relaxation of the flexors occurring concurrently with contraction of the extensors. This co-ordination I term "*reciprocal innervation.*"

That when the flexors of knee and hip are reflexly thrown into action the extensors are inhibited, seems proved by the *impossibility* of obtaining the crossed reflex in the extensors when the foot of the crossed side is pinched.

Again, on two occasions, once in Cat and once in *Macacus*, the leg lying at the time in a state of rigidity due to tonic spasm of the extensor muscles of hip and knee, gentle excitation of the central end of a twig of the internal saphenous nerve at the ankle at once produced *relaxation* of the extensors, and at the same time some contraction of the flexors. In each case the phenomenon is one of regular occurrence so long as the conditions are regularly repeated. This leads me to return to the phenomena mentioned above at p. 171. These, in illustration of the existence of the long uncrossed paths in the bulbo-spinal axis, pass from bulb and cerebellum, even through great lengths of the cord. It is obvious that for evidence of inhibition it is supremely important to have a steady condition of activity pre-existent in the tissue to be examined. Inhibition in muscle has for its sign relaxation. Relaxation predicates contraction, tonic, or otherwise. Upon prepontine transection (Rabbit, Cat) ensues what I have termed above *decerebrate rigidity*, which affects the

* 'PFLÜGER'S Archiv,' vols. 8 and 9.

† SHERRINGTON, 'Journ. of Physiol.,' vol. 13, p. 722, Plate 23, 1892.

extensors of knee, elbow, and back, and to a less extent ankles, but not wrists, and includes neck and tail, pre-eminently. HUGHLINGS JACKSON has laid stress on the cerebellum as a source of muscular tonus. In the phenomenon of "decerebrate rigidity" the cerebellum *may* be an ultimate source of the rigidity, and right-hand semi-section of the bulb above the decussation of pyramids destroys the right-hand rigidity. It must arise from an uncrossed influence arising somewhere above the lowest third of the IVth ventricle and below the cerebral hemispheres. The state of contraction appears akin to ordinary tonus. Its reflex origin is evidenced by its severe or even total depression on severance of appropriate afferent spinal roots (p. 157). Thus the hypertonic condition of rigidity almost or quite vanishes from left triceps when the left afferent brachial roots are cut, from left quadriceps extensor cruris when left lumbo-sacral afferent roots are cut. The rigidity is a persistent condition for many hours; I have seen it persist for four days. It is so forcible that the animal can be placed erect on the four feet. Semi-section of cord abolishes it on the same side below the lesion, so also does semi-section of the bulb above the pyramidal decussation. It is lowered or temporarily abolished by deep chemical anæsthesia, sufficient to abolish ear-reflex (Cat) or knee-jerk. With this hypertonic rigidity as background, inhibitions, relaxations, can be produced in these muscles. The graphic records taken in the ordinary way show that the excitations which reflexly cause contraction of the flexors, cause synchronous relaxation—often even to post-mortem length—of the extensor muscles. Thus: from skin of fore-paw, from dorsal cutaneous branch of ulnar nerve, from funiculus cuneatus at the calamus, from side of superior vermis contraction of biceps, relaxation of triceps of same side; from hind-paw, from internal saphenous nerve, from funiculus gracilis, side of superior vermis, contraction of the hamstrings, relaxation of the quadriceps extensor cruris of same side. At the crossed elbow occurs (Rabbit, Cat, Dog, Monkey) conversely some relaxation of flexors of knee and elbow and increase of existing contraction in extensors. At the crossed knee similarly occurs (Cat, Dog, Monkey) extension (with extension of ankle) that is increased contraction of extensors with further relaxation of flexors; but in Rabbit, in my experience, flexion at the crossed knee concurrently with flexion at the same side knee, and some extension at both ankles is the rule. The concurrence in reply to one and the same excitation of inhibition of one component of an antergetic couple with contraction of the other component occurs in these instances as in the reactions of the lateral eye-muscles.* It is indeed a complete example of what I have described as "reciprocal innervation."

Allied to the above examples is the following:—Excitation of the central end of the afferent root of the VIIth cervical nerve, at times provokes extension at the elbow, but more often flexion: when extension is obtained the flexors lie absolutely without active contraction, and if in tonic rigidity at the time are,

* 'Proc. Roy. Soc.', vol. 52, 1892. SHERRINGTON; and 'Journ. of Physiol.,' vol. 17, 1894.

inhibited, actively relaxed. The two effects, namely, reflex flexion of elbow and reflex extension of elbow sometimes succeed each other in the course of repetition of excitations even in the same few minutes. The condition indicates the incompatibility of the contraction or pressor action (augmentor action) of the two groups of muscles under spinal reflex action: if one group is selected for increased (augmented) action the other is left severely alone, or if tonic contraction be going on in it, it is subjected to depression of action (inhibition). The carrying out of a movement by the overpowering of the active contraction of one muscle-group by the active contraction of another muscle-group, is throughout my experience *foreign to the tactical mechanism of the spinal cord.* This experience harmonises in part with an idea put forth some years ago by H. MUNK,* and made the subject of a research undertaken at his instigation by SCHLOESSER.† In short, my observations prove the existence of "reciprocal innervation" of antagonistic muscles as part of the machinery of spinal reflexes, and point to it as possibly a widely extensive part of that machinery. It not only affects contrasted muscle-groups, but also contrasted parts of one and the same muscle as in *quadriceps ext. fem.* and in *triceps brachii.*

PHASIC VARIATION IN THE REFLEX ACTIVITY OF THE CORD.

Although, as the "rule of monotonous repetition" above states, absence of variation of the movement elicited by repetitions of a particular stimulus is a striking character of spinal reflexes in the Mammal and lends to them a machine-like quality of regularity, there does occur a curious variety of result when they are examined in the same individual from day to day. The very spot of skin that one day evokes constantly flexion of all the toes, may the following day evoke nothing but flexion of hallux and extension of the other toes, and the day following may evoke nothing, or again, only the movement obtained three days before. A stimulus usually eliciting dorso-flexion at ankle, may on some days elicit in the same individual, plantar flexion of ankle. As a broad rule, it is certain that spinal reflexes are more easily elicited when a well-nourished animal is hungry and expectant of food, and less easily after a heavy meal. Altogether apart, however, from feeding time on some days hardly a reflex can be elicited from the very animals that on other days yield a variety with readiness. Conditions of individual age, and especially of general nutrition, influence, as FREUSBERG points out for the lumbo-sacral reflexes of the Dog, the facility of reflexes very greatly indeed.

[POST-SCRIPTUM, *June*, 1898.—I seize a final possibility afforded to append a brief sentence of mention and appreciation of the admirable work of BOLK just appearing ('Morpholog. Jahrbuch,' vol. 25, 4, p. 465, 1898; vol. 26, 1, p. 91, 1898), on the

* 'Verhandlungen der Berliner Physiologischen Gesellschaft,' October, 1881.

† 'Archiv f. Physiologie,' DU BOIS-REYMOND, Berlin, 1880.

morphological portion of the subject-matter of this paper. Had the dates permitted, I should have amplified the text by collating in it the results he obtains in Man with those to which I have come in Macacus. His labours perform for human anatomy a service that has been long wanted and wanting. Had such work existed at the time my researches were made, they would have rendered mine the utmost assistance. As it is, it gives me gratification to find our independently-attained results, reached by such different methods of inquiry, are as generally harmonious as they appear to be. Professor BOLK's work strengthens my view, expressed at the end of Section I. of this paper, pp. 91, 92, that *the forelimb of Man is segmentally prefixed as compared with that of Macacus and of the other animal species enumerated.* My researches commenced from the caudal end of the body and went headwards; Professor BOLK conversely has commenced with the top of the cervical region, and is working downwards. Hence the final part of my research and the beginning part of his overlap. As the mutual value of each is partly due to its independence of the other, I may, perhaps, state that my delimitations of the skin-fields of the cranio-spinal nerves of head, neck, and arm were in a series of photographs demonstrated by me to the Neurological Society of London, Feb. 9th, 1893 (see 'Proc. Neurol. Soc.,' p. 23, 'Brain,' Spring Number, 1894), and that some figures of the same from my photographs appeared in illustration of my friend, Dr. HENRY HEAD'S, second paper on Sensory Disturbances, especially in reference to Visceral Disease, published in 'Brain,' 1895. But Professor BOLK'S work has been altogether independent of these partial publications of mine. In his papers we have the best and first really adequate study of the segmental morphology of the human limbs.

Section IV. of the foregoing communication formed the material of the Croonian Lecture, on "The Mammalian Spinal Cord as an Organ of Reflex Action," which I delivered before the Society, April 1, 1897.]

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DESCRIPTION OF PLATES.

PLATE 3.

Fig. 1. The posture assumed in decerebrate rigidity, p. 159 and p. 174 in text.

Figs. 2-17 inclusive are photographs of *Macacus rhesus*: in all the white side of the demarcation line is toward the field whence reflex responses were obtained, the black side toward the field of anæsthesia.

Fig. 2. The anterior border of the skin-field of the IInd nerve.
Fig. 3. The borders of the IVth and VIIIth cervical and the IVth thoracic skin-fields.
Fig. 4. Borders of IInd and Vth cervical and of IInd and VIth thoracic skin-fields.
Fig. 5. Border of VIth cervical skin-field.
Fig. 6. Borders of IInd and VIth cervical and IInd thoracic skin-fields.
Fig. 7. Borders of IIIrd and VIIth cervical skin-fields.
Fig. 8. The same, with IIIrd thoracic as well.

PLATE 4.

Fig. 9. Borders of IVth cervical and VIIIth cervical skin-fields.
Fig. 10. Borders of IIIrd and VIIIth cervical skin-fields.
Fig. 11. Borders of VIIIth cervical and IVth thoracic skin-fields.
Fig. 12. Borders of the VIIIth cervical and IIIrd thoracic skin-fields.
Fig. 13 Borders of the IIIrd cervical, VIIIth cervical, and IIIrd thoracic skin-fields.
Fig. 14. Borders of IIIrd cervical and VIIIth cervical skin-fields.
Fig. 15. Borders of IVth cervical, VIIIth cervical, and IVth thoracic skin-fields.
Fig. 16. Borders of IVth cervical, and Ist and VIth thoracic skin-fields.
Fig. 17. Borders of Ist thoracic and VIIth thoracic skin-fields.

PLATE 5.

Fig. 18. Model from a cast of *Macacus rhesus*, to show the borders of the skin-fields of the cranial and upper spinal nerve roots. On the left side the anterior borders only, on the right the posterior borders only. The position of the mid-ventral line of the limb is marked.

Fig. 19. Same. The mid-dorsal line of the limb is marked.

Fig. 20. Same, from behind. The mid-dorsal line is seen.

Fig. 21. Same, from the front. The mid-ventral line of the limb is seen.

PLATE 6.

The field of anæsthesia occasioned by resection of a piece of the sciatic trunk under the glutæus muscle. See p. 102 in text. Figs. 1, 2, 3, the front, the back, and sole respectively.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

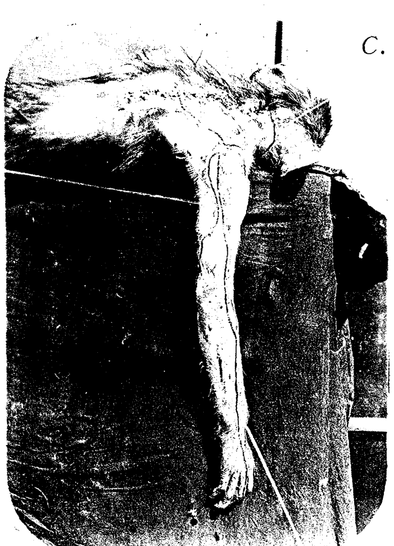


Fig. 6.

Fig. 7.

Fig. 8.

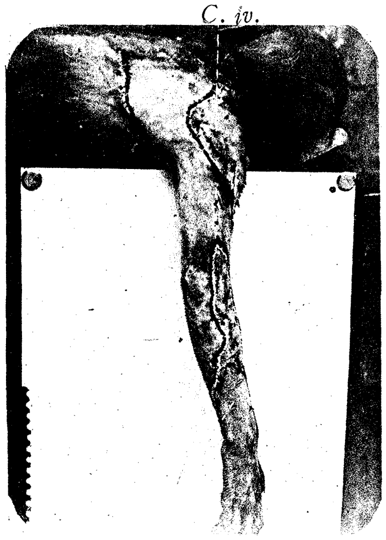


Fig. 9.

Fig. 10.

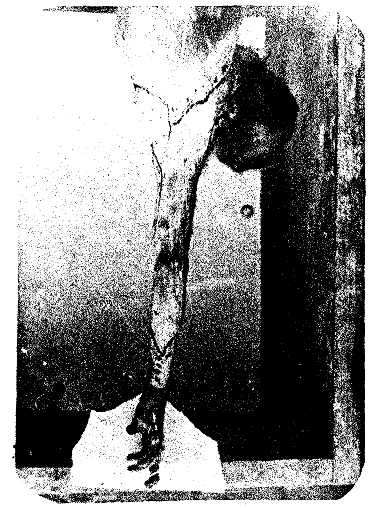


Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.

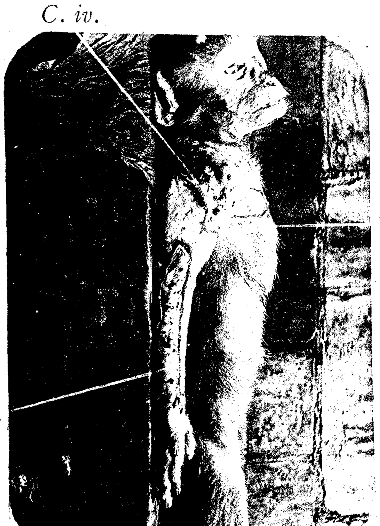


Fig. 15.

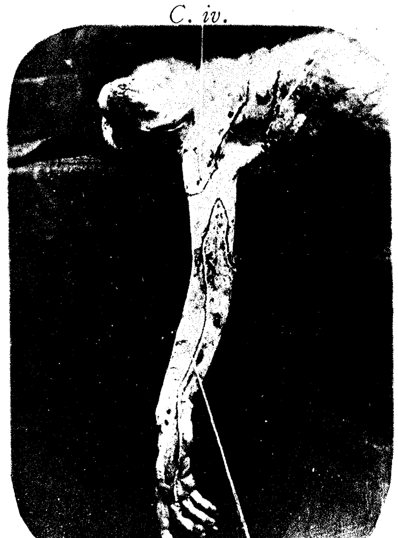


Fig. 16.

Fig. 17.

Fig. 18.

Fig. 19.

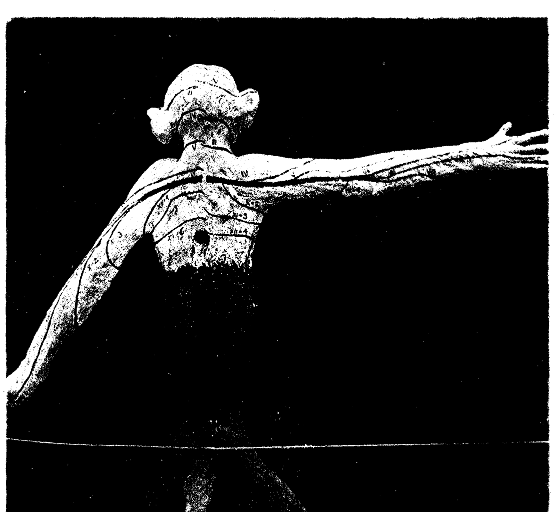
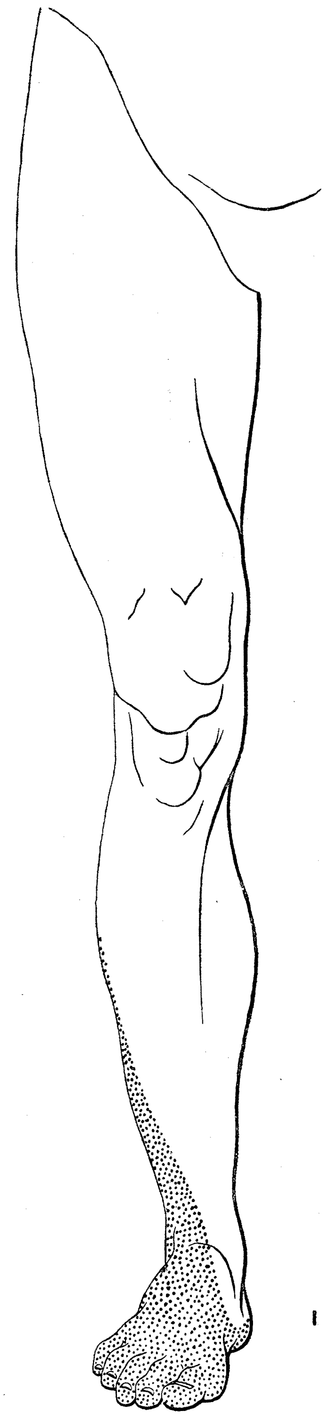
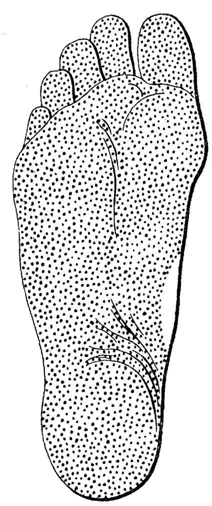


Fig. 20.

Fig. 21.



1



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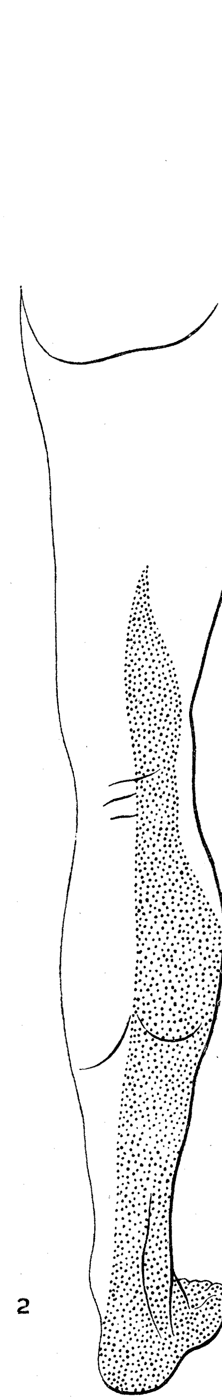


2

	IInd Thoracic	Ist Thoracic	VIIIth Cervical	VIIth Cervical	VIth Cervical	Vth Cervical
Back and trunk	Erector spinæ	Erector spinæ	Erector spinæ	erector spinæ	Erector spinæ	Erector spinæ
	levator costæ	levator costæ	longus colli	longus colli	longus colli	longus colli
	transverso-spinales	transverso-spinales	transverso-spinales	transverso-spinales	transverso-spinales	transverso-spinales
					diaphragma	diaphragma
						levator anguli scapulæ
Shoulder					rhomboidei	rhomboidei
	serratus posticus sup.	serratus posticus sup.				
					subclavius	subclavius
	intercostales	intercostales				
				serratus magnus	serratus magnus	serratus magnus
	scaleni	scaleni	scaleni	scaleni	scaleni (not always)	scalenus medius
				deltoid (spinous portion)	deltoideus	deltoideus
				teres minor	teres minor	teres minor
			teres major	teres major	teres major	
				subscapularis	subscapularis	subscapularis
				supraspinatus	supraspinatus	supraspinatus
				infraspinatus	infraspinatus	infraspinatus
		pectoralis minor	pectoralis minor	pectoralis minor		
		pectoralis major (lower edge only)	pectoralis major {sternal part more than clavicular}	pectoralis major {clavicular, sternal}	pectoralis major {clavicular, sternal}	pectoralis major (clavicular)
		latissimus dorsi	latissimus dorsi	latissimus dorsi	latissimus dorsi	
Arm				biceps (slight)	biceps	biceps
				brachialis anticus (slight)	brachialis anticus	brachialis anticus
			coraco-brachialis	coraco-brachialis	coraco-brachialis	coraco-brachialis
		triceps, (especially its inner head)	triceps	triceps	triceps (outer and long head)	
			anconeus	anconeus		
Forearm			extensor carpi rad. brevior	extensor carpi rad. brevior	extensor carpi rad. brevior (slight)	extensor carpi rad. brevior (slight and occasional)
			pronator radii teres	pronator radii teres	pronator radii teres (slight)	
		extensor indicis	extensor indicis	extensor indicis		
		extensor communis digitorum	extensor communis digitorum	extensor communis digitorum	extensor communis digitorum	
		flexor carpi ulnaris	flexor carpi ulnaris	flexor carpi ulnaris (v. slight)	flexor carpi ulnaris	
		flexor carpi radialis (very slight)	flexor carpi radialis	flexor carpi radialis	flexor carpi radialis	
		extensor brevis pollicis	extensor longus pollicis	extensor longus pollicis	extensor longus pollicis	
		extensor longus pollicis	extensor brevis pollicis	extensor brevis pollicis		
		extensor oss. met. pollicis	extensor metacarpi pollicis	extensor metacarpi pollicis	extensor oss. metacarpi pollicis	
		extensor carpi ulnaris	extensor carpi ulnaris	extensor carpi ulnaris		
				extensor carpi rad. longior	extensor carpi rad. longior	extensor carpi rad. longior
		extensor minimi digiti	extensor minimi digiti	extensor minimi digiti		
				supinator brevis	supinator brevis	supinator brevis
				supinator longus	supinator longus	supinator longus (slightly)
	palmaris longus	palmaris longus	palmaris longus	palmaris longus		
	flexor longus pollicis	flexor longus pollicis	flexor longus pollicis	flexor longus pollicis	flexor longus pollicis (a few fibres)	
	pronator quadratus	pronator quadratus	pronator quadratus	pronator quadratus		
	flexor sublimis digitorum	flexor sublimis digitorum	flexor sublimis digitorum	flexor sublimis digitorum (slight)		
	flexor profundus digitorum	flexor profundus digitorum	flexor profundus digitorum	flexor profundis digitorum		
Hand		superficial short muscles of thumb	superficial short muscles of thumb	superficial short thumb muscles		
	deep short muscles of thumb	deep short muscles of thumb	deep short muscles of thumb			
	lumbricales	lumbricales	lumbricales, 1, 2, 3	lumbricales, 1, 2		
	interossei {dorsal, palmar}	interossei {dorsal, palmar}	interossei {dorsal, all; palmar, 1, 2, 3}	interossei, 1, 2		
	short muscles of little finger	short muscles of little finger	short muscles of little finger			

- —— nerve fibres degenerate regularly on section of root.
- —— nerve fibres degenerate occasionally on section.
- —— contracts regularly on stimulation of root.
- —— contracts occasionally, *i.e.*, in some individuals.

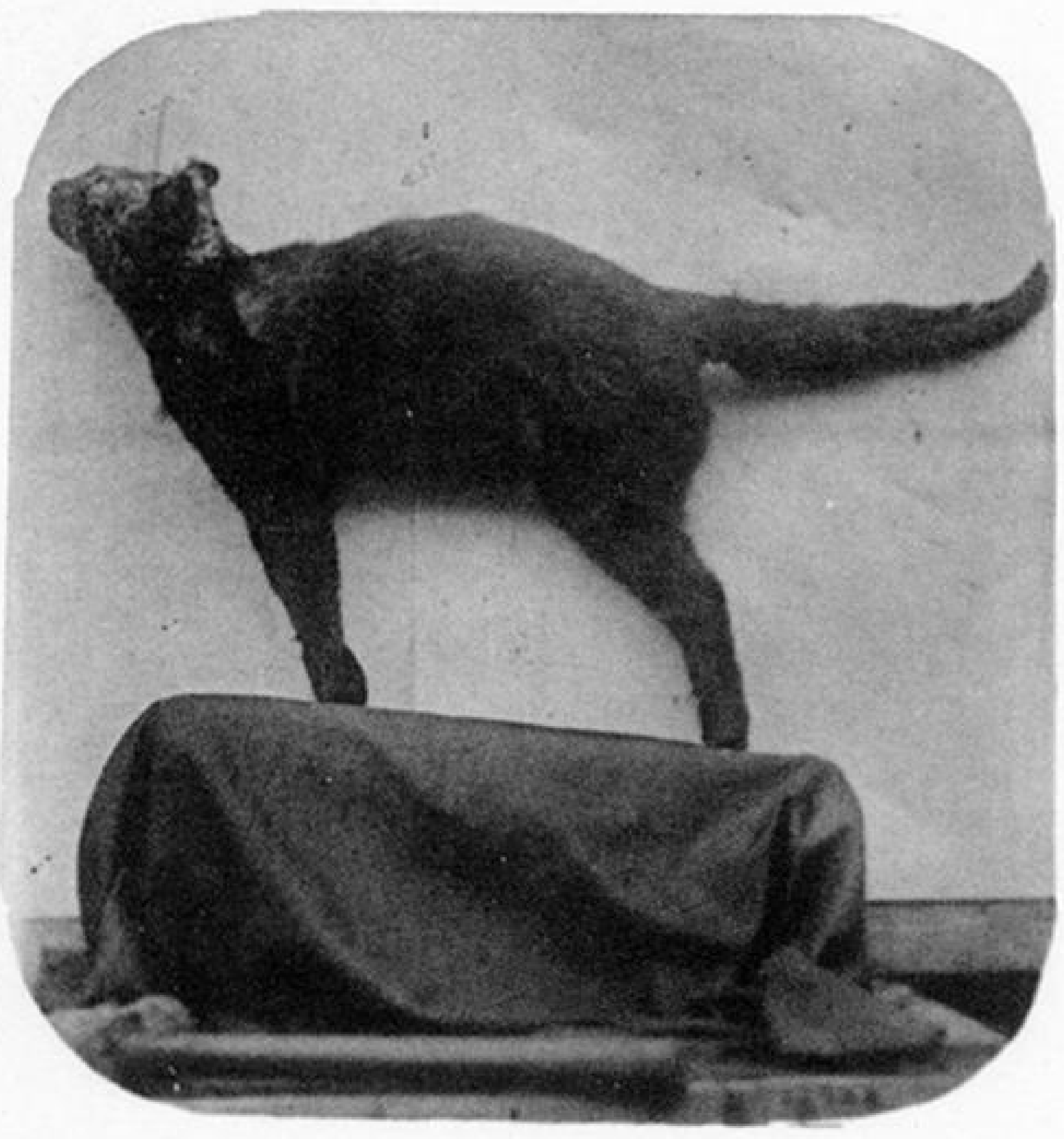


Fig. 1.

Fig. 2.

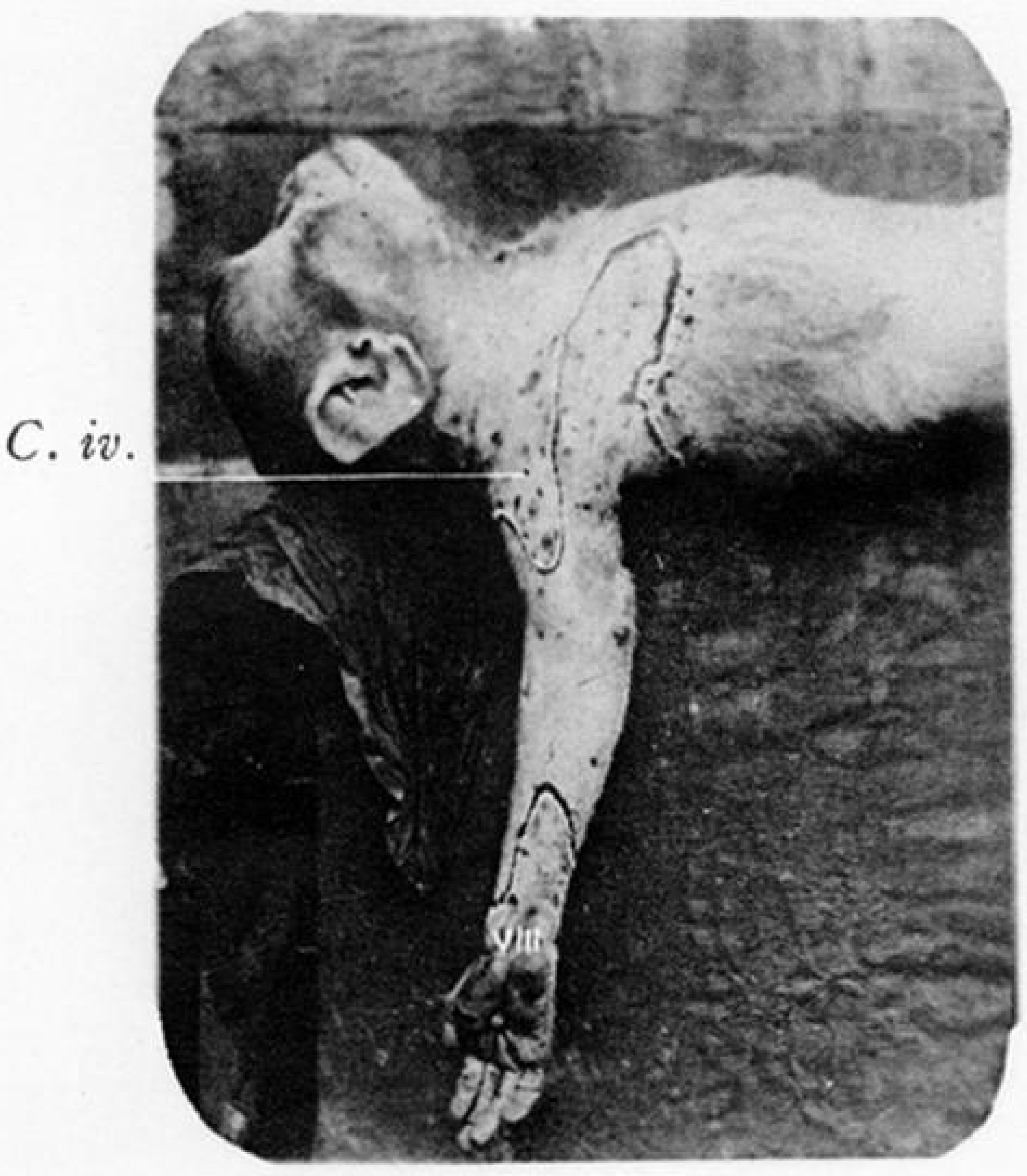


Fig. 3.

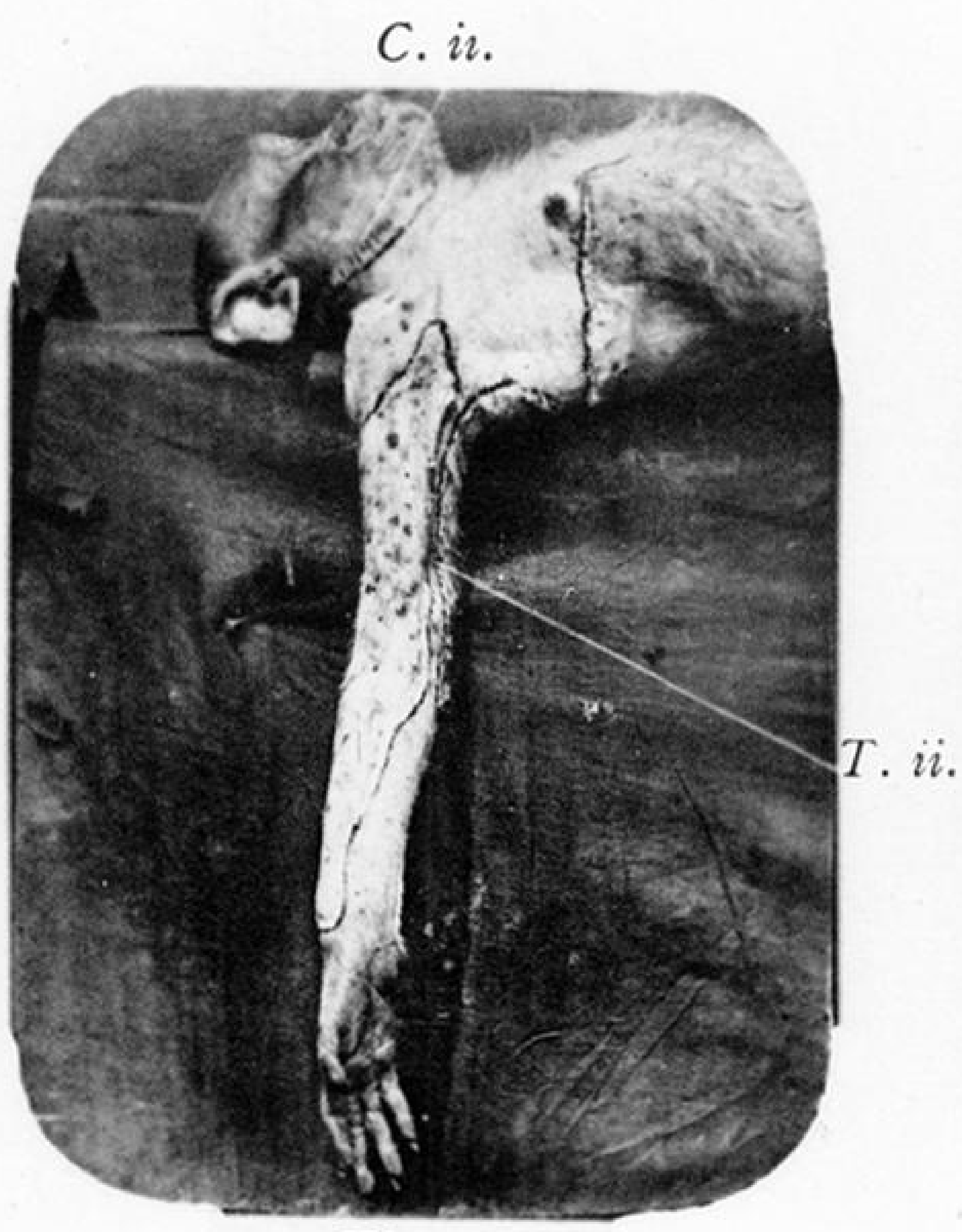
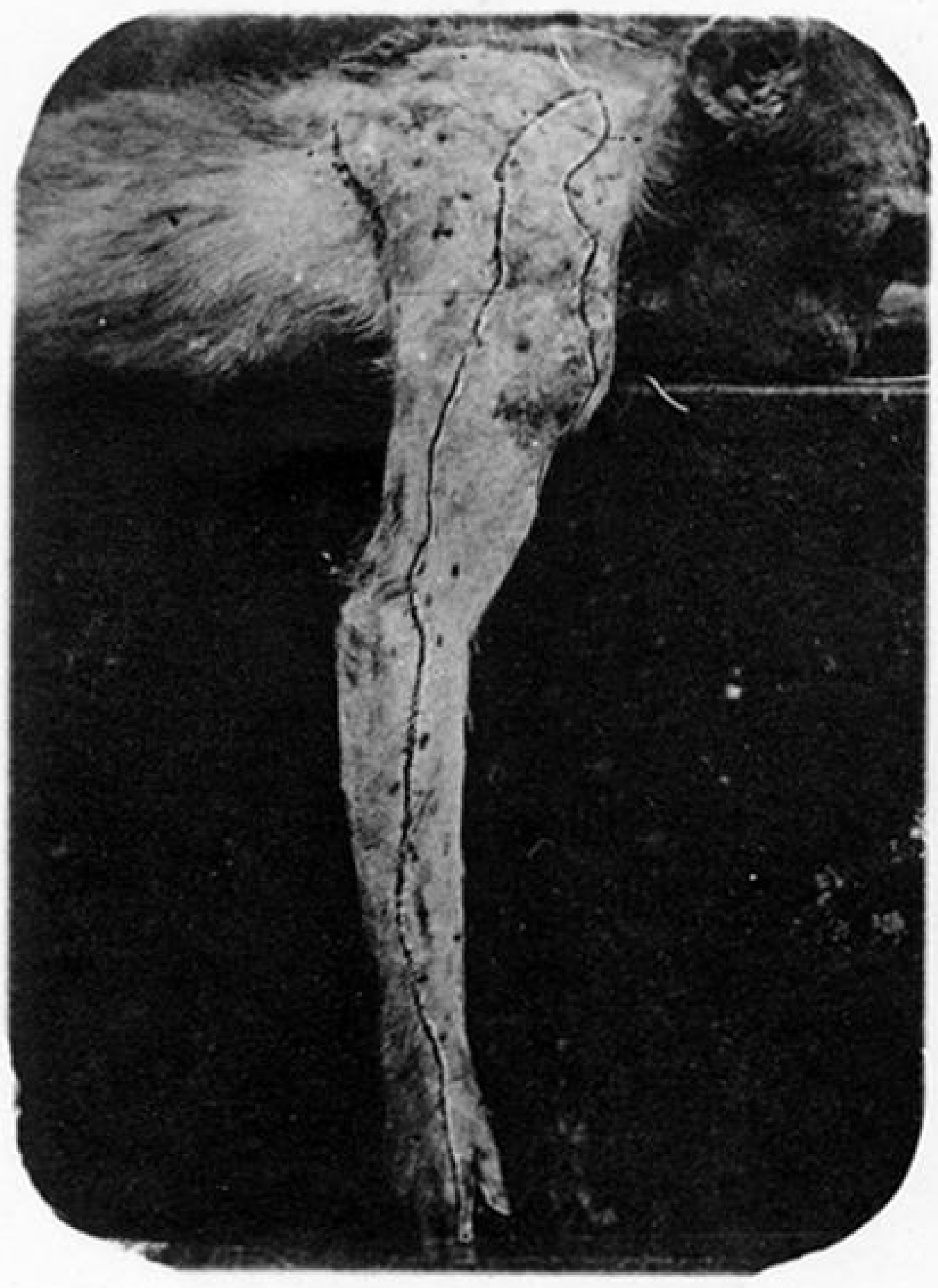


Fig. 4.



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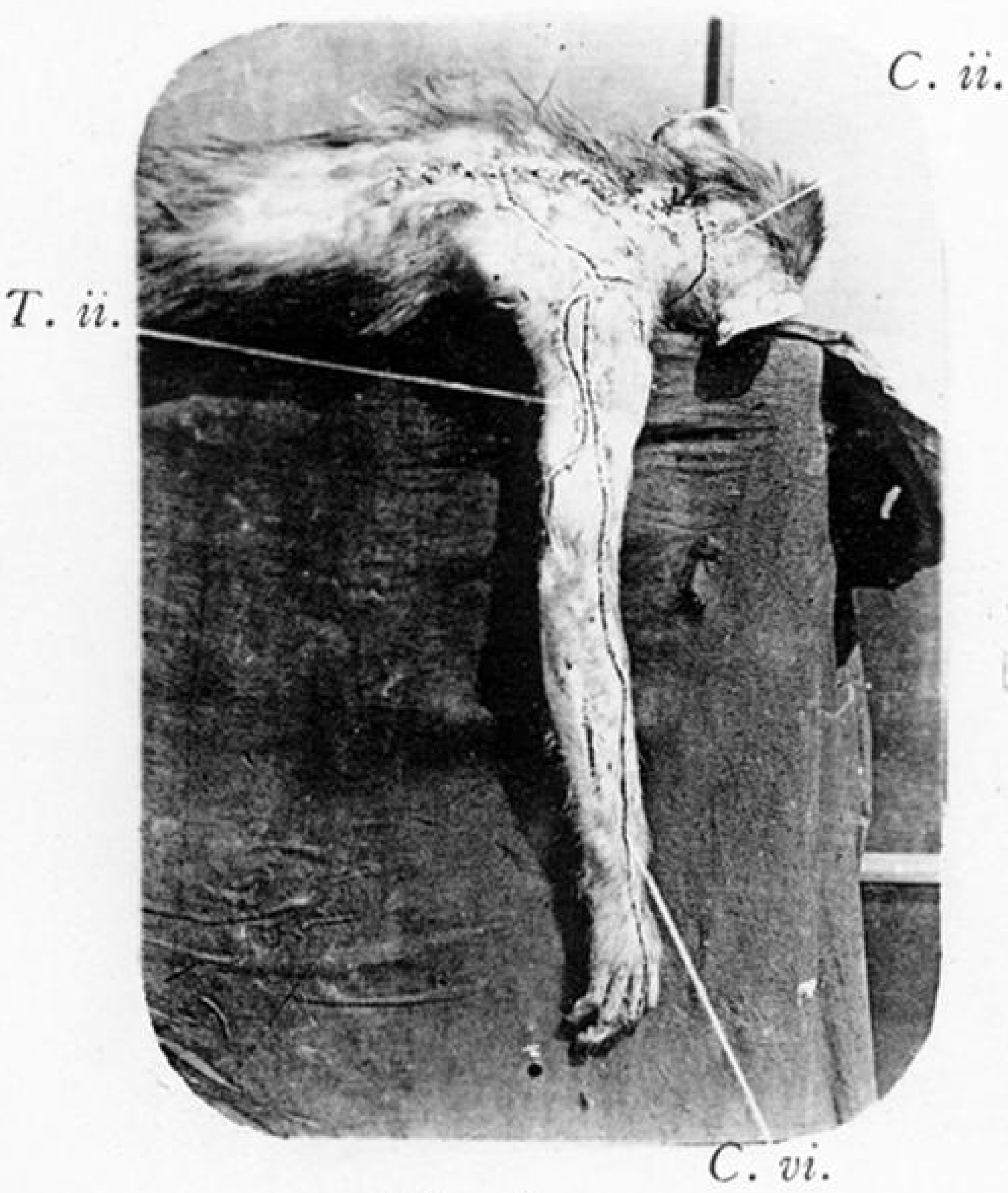

Fig. 6.

Fig. 7.

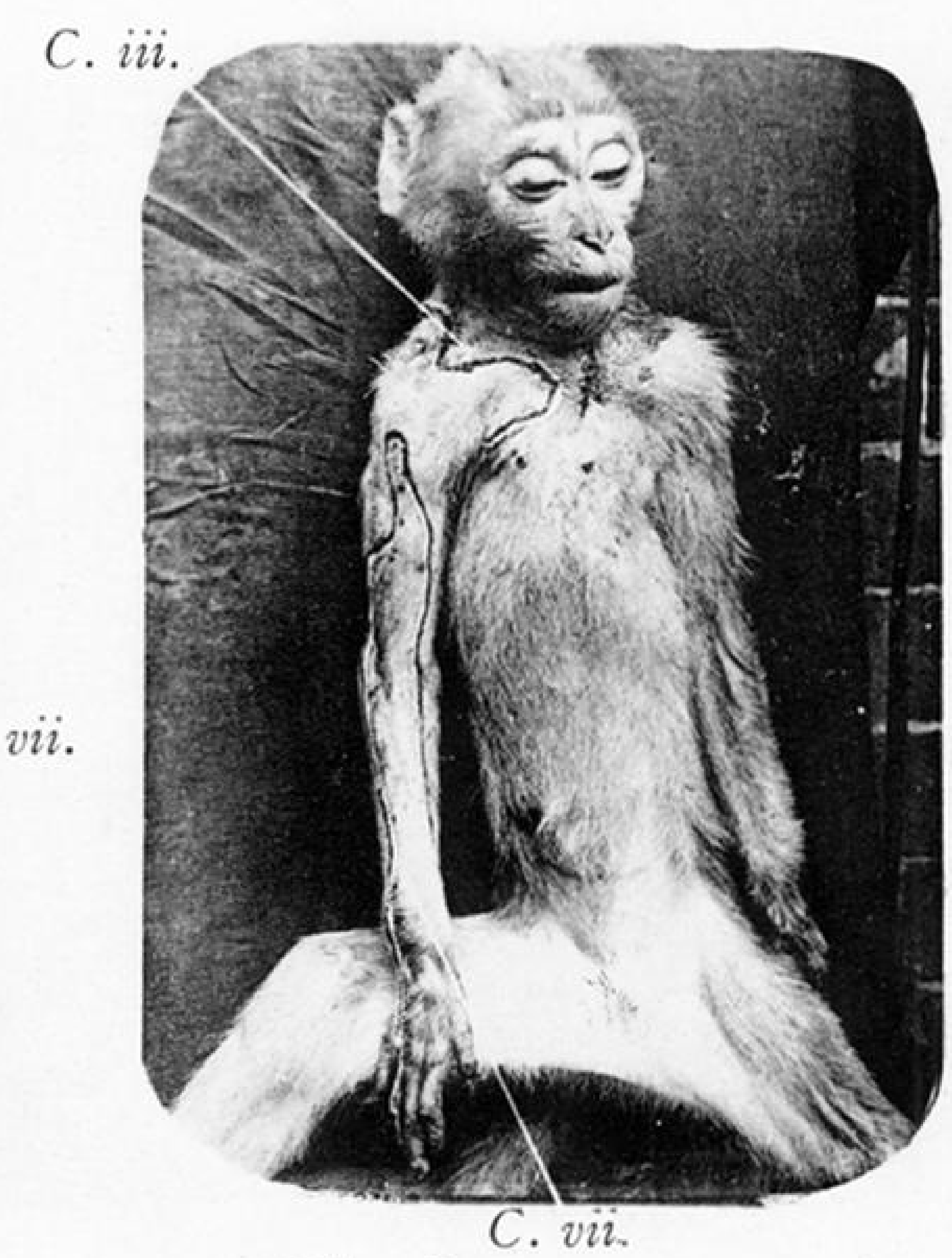

Fig. 8.

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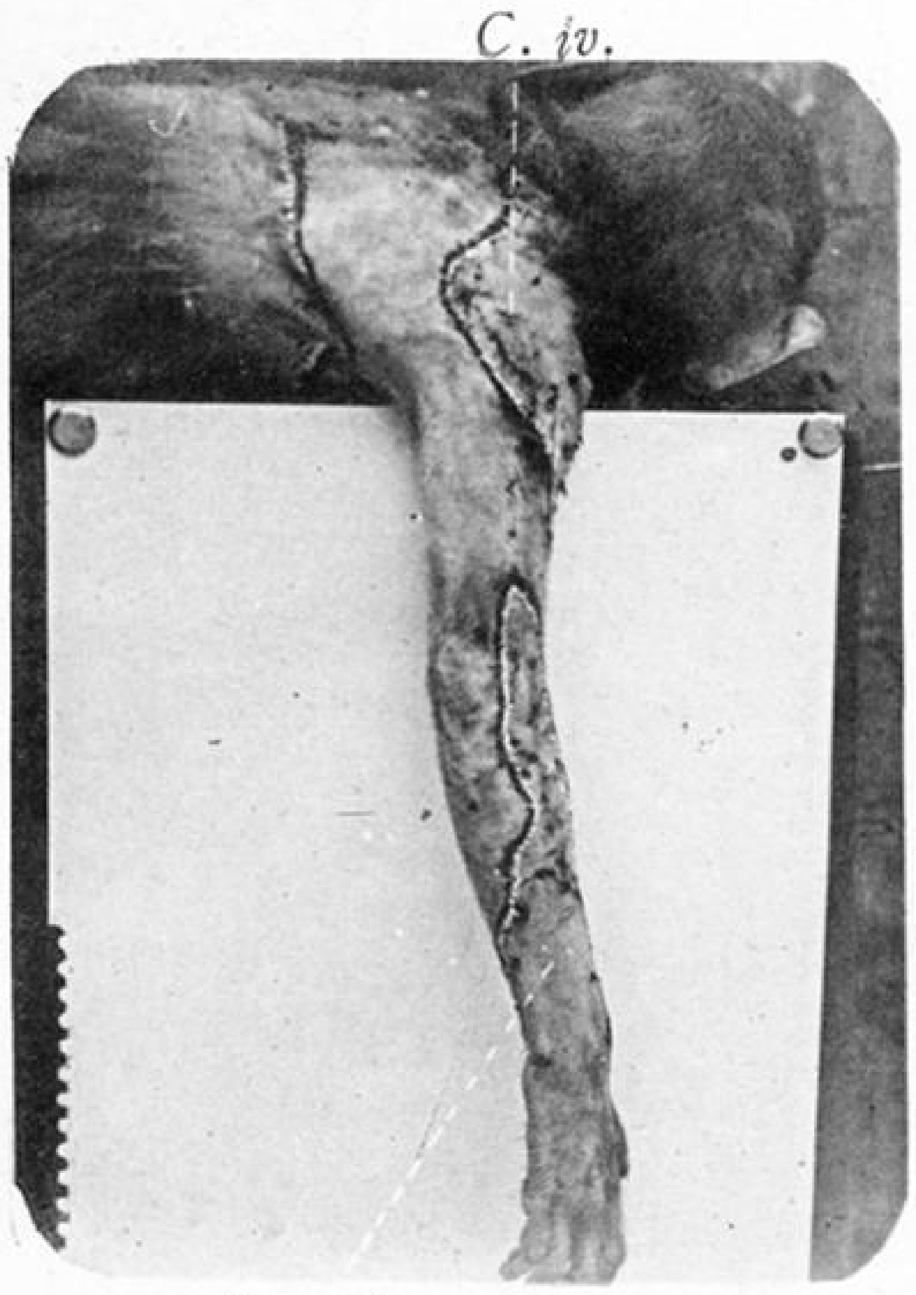


Fig. 9.

Fig. 10.

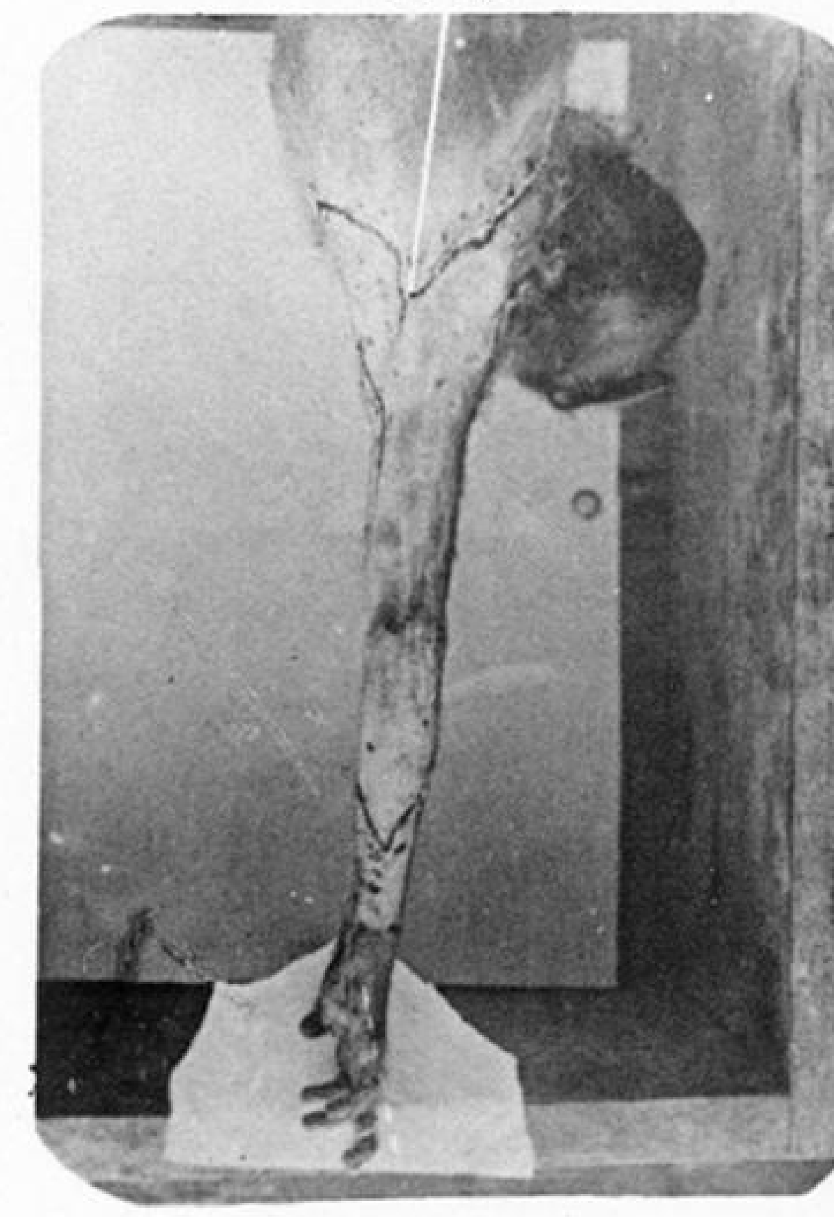


Fig. 11.

Fig. 12.

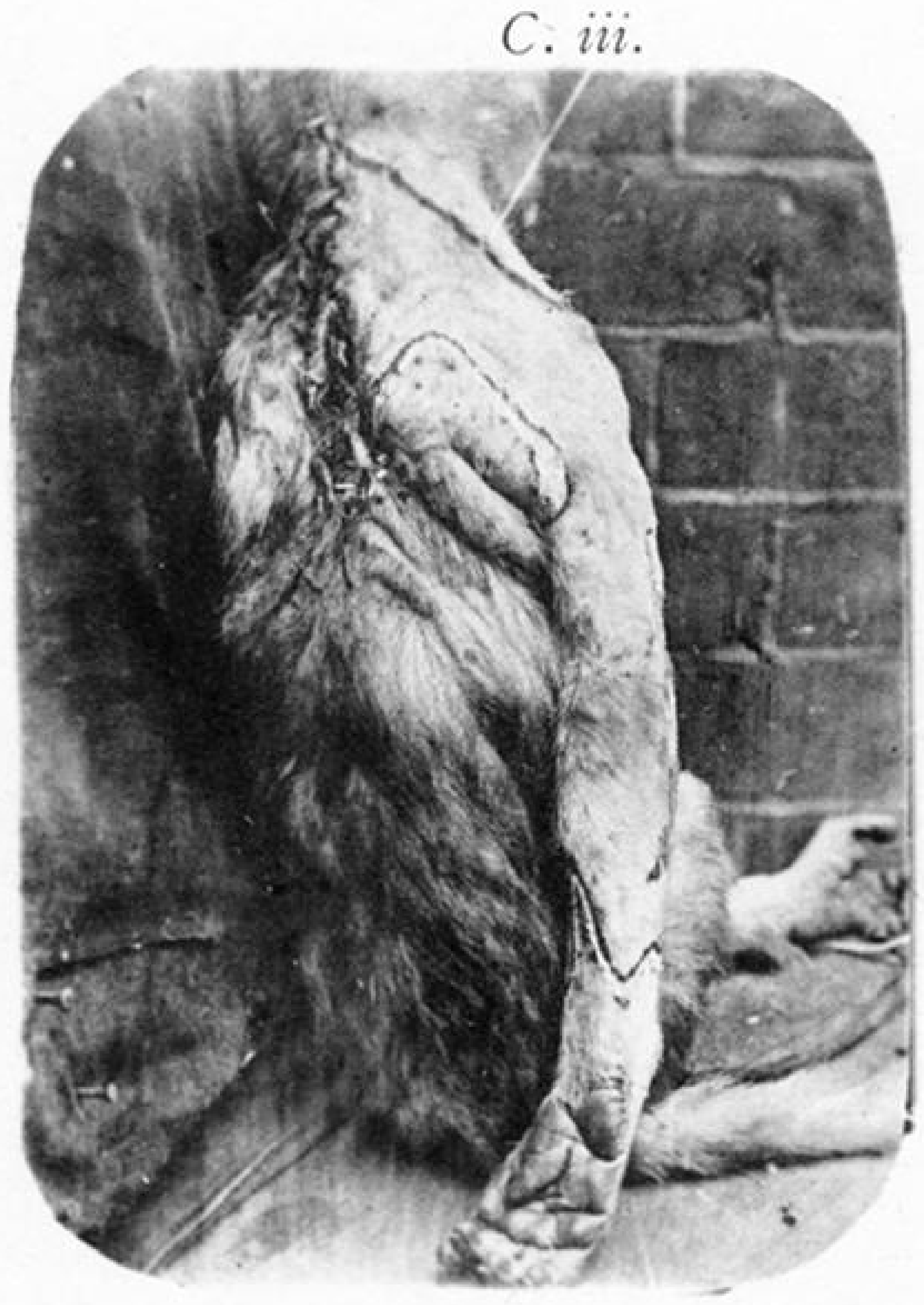
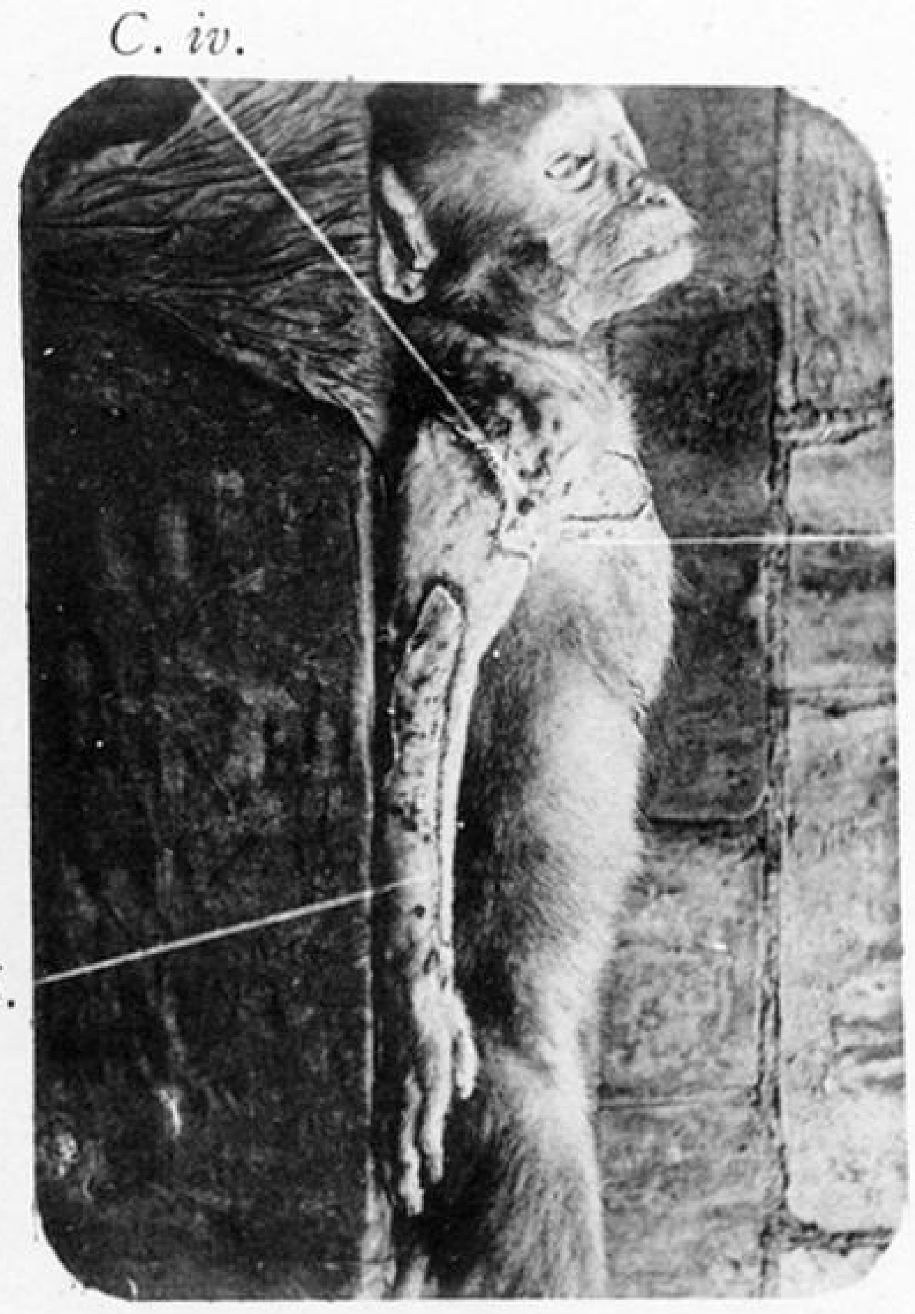


Fig. 13.

Fig. 14.



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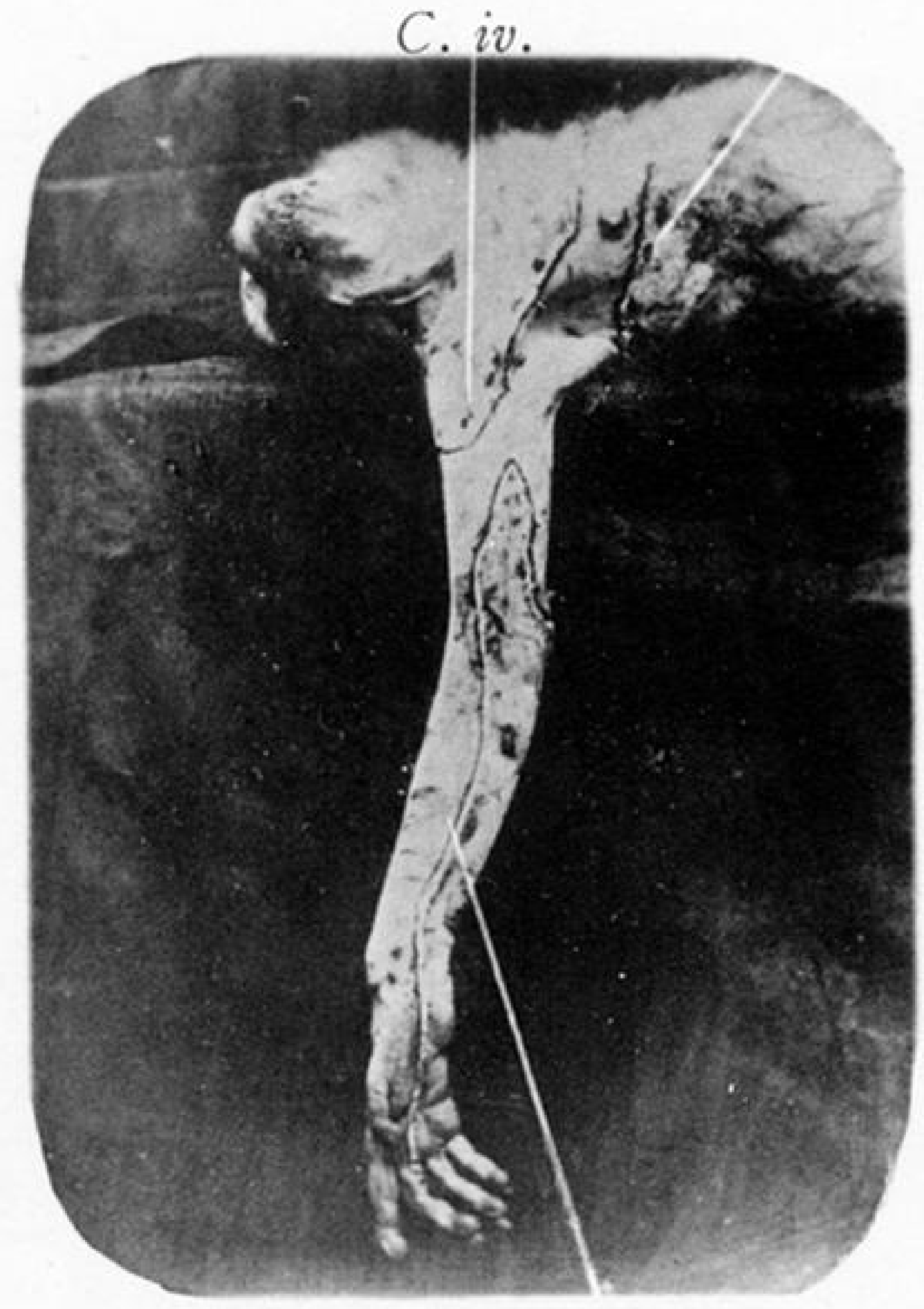

Fig. 16.

Fig. 17.

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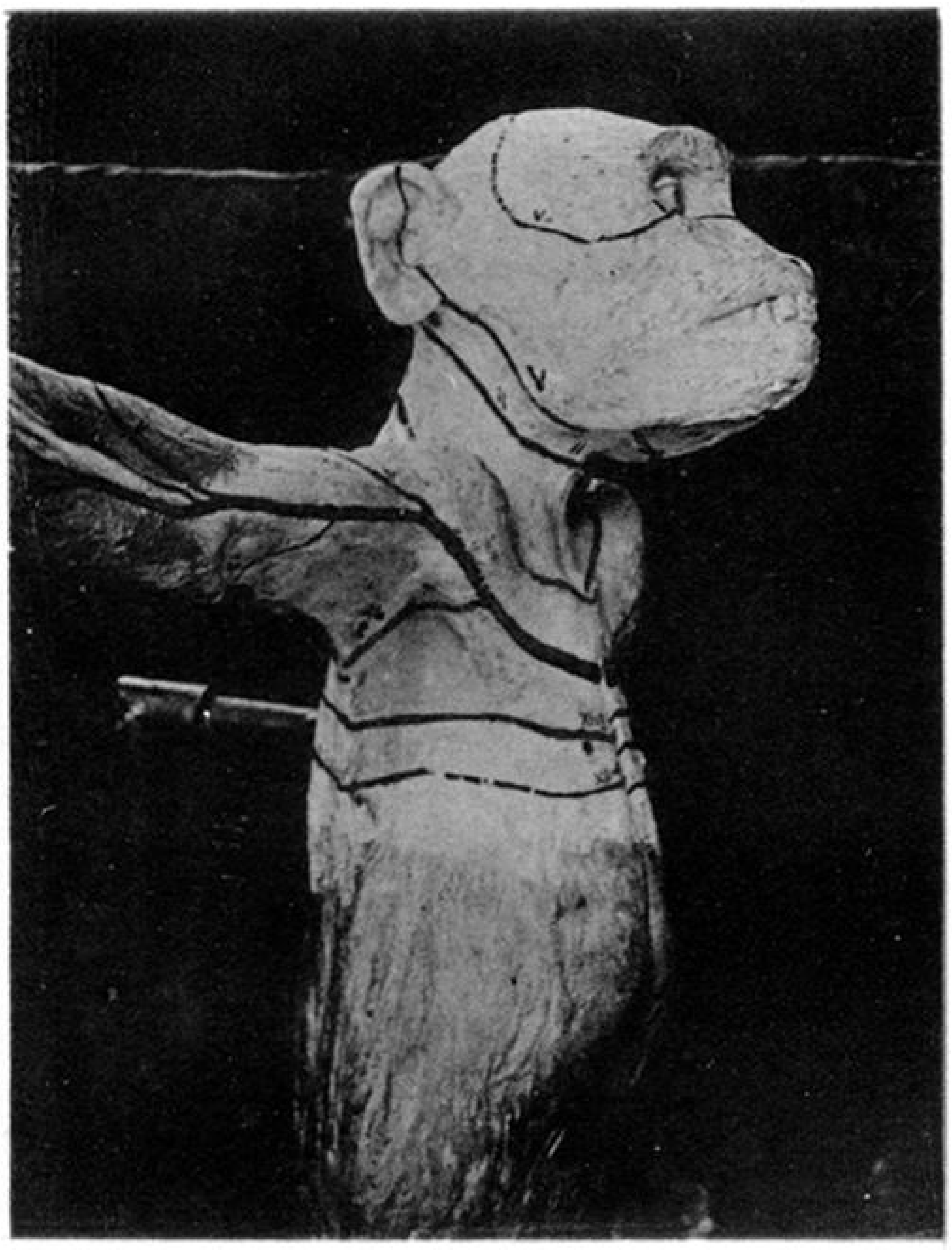

Fig. 18.

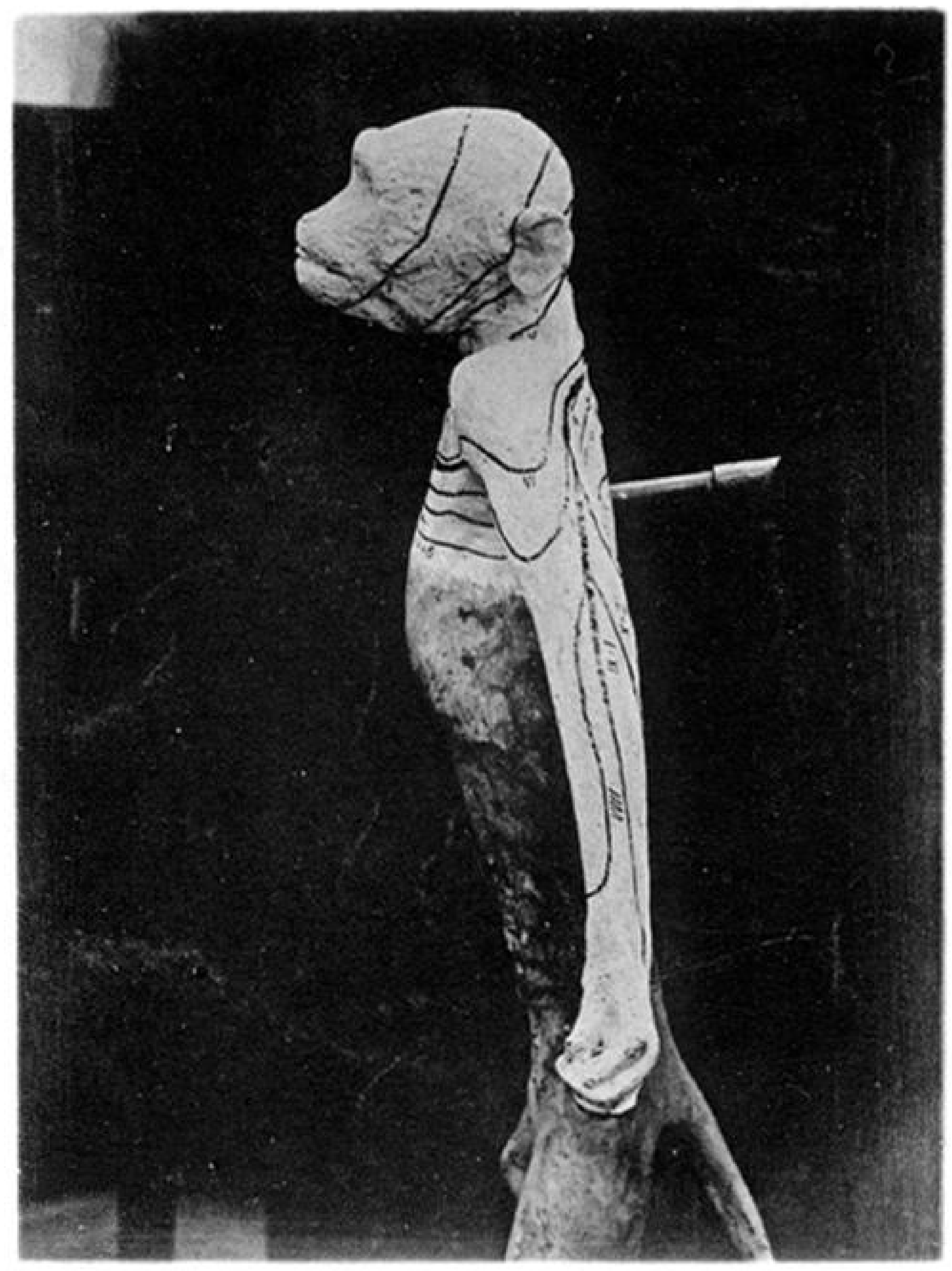

Fig. 19.

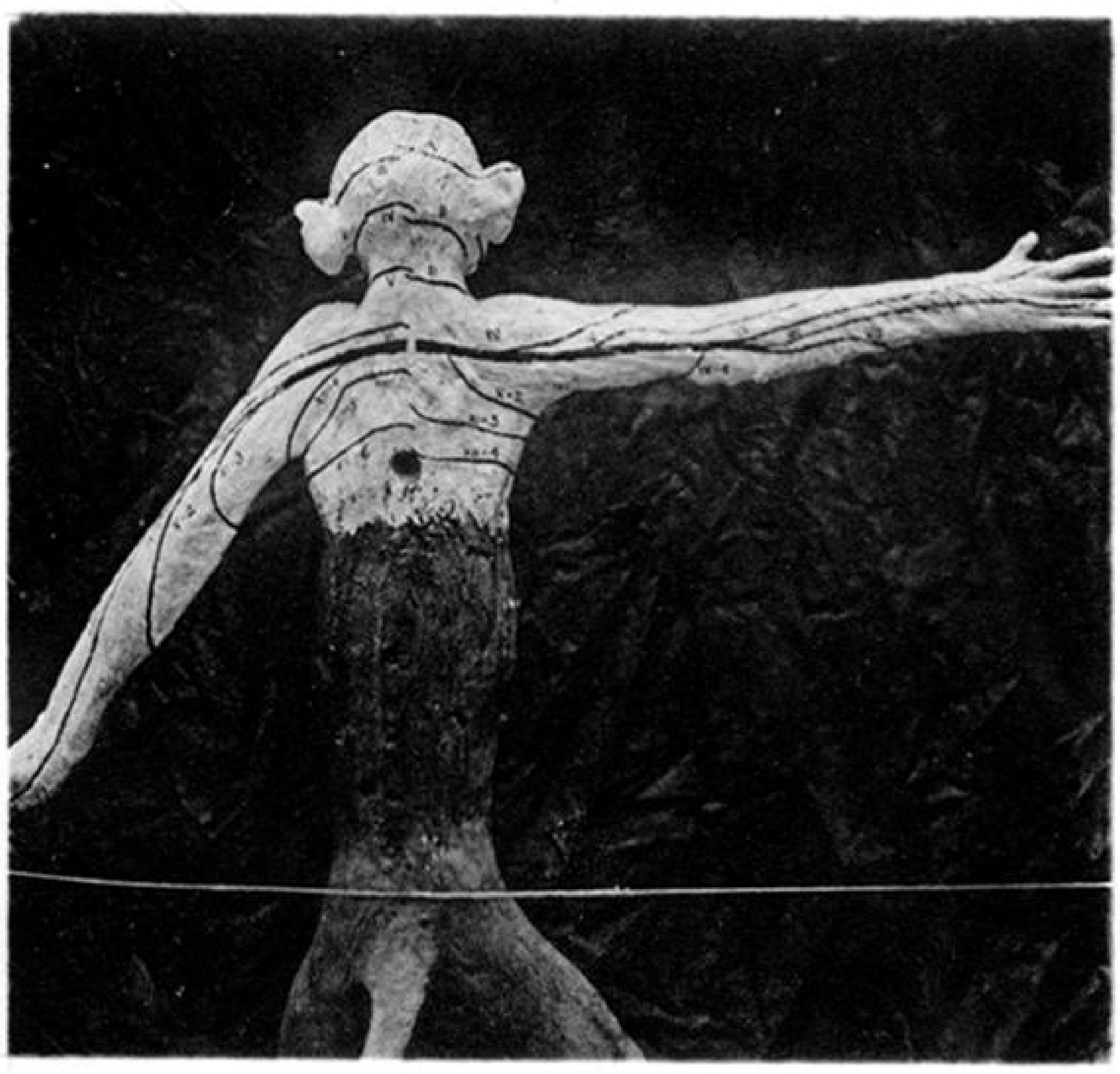

Fig. 20.

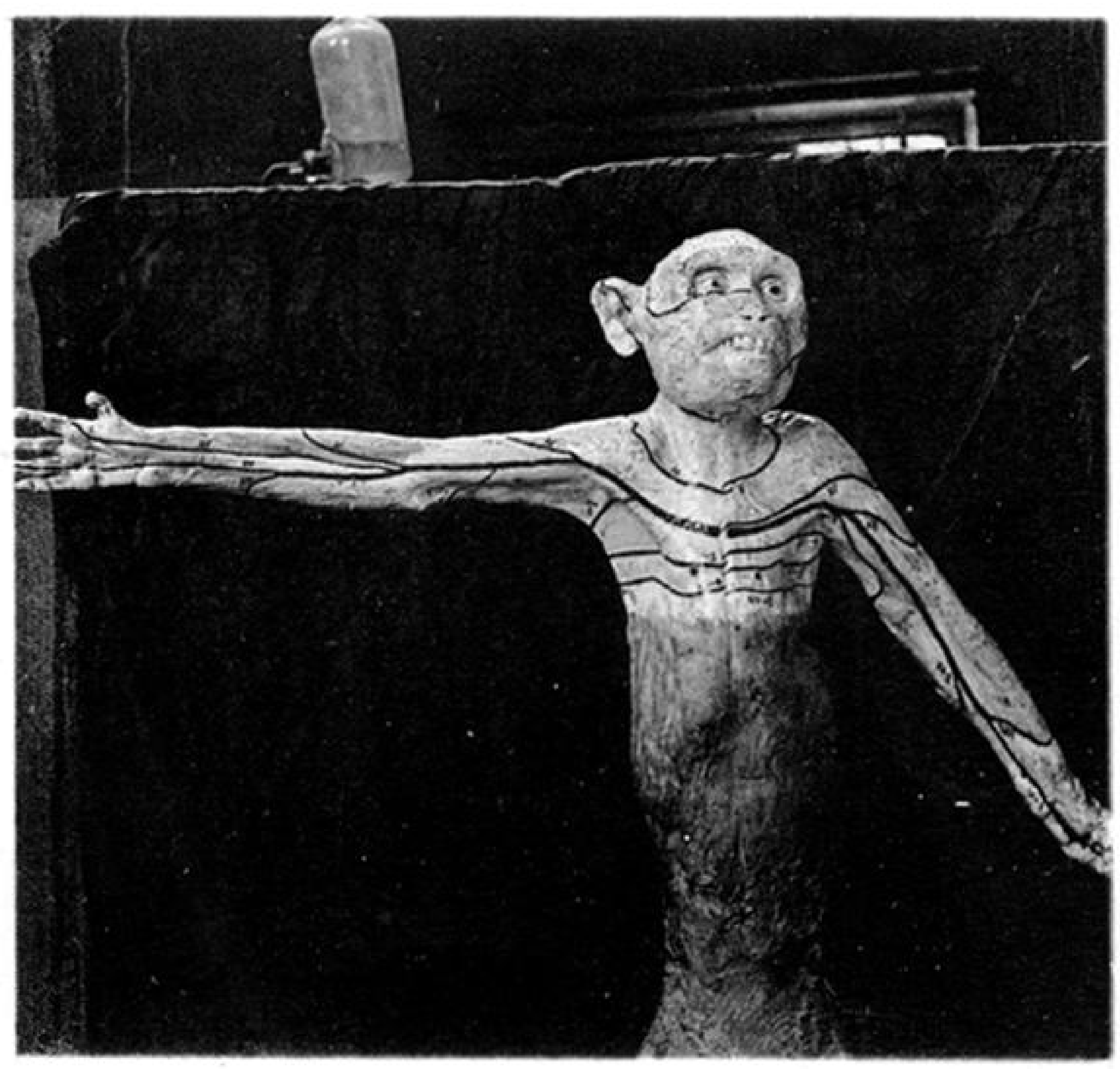

Fig. 21.

PLATE 5.

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