XIII. *On certain Functions of the Spinal Chord, with further Investigations into its Structure.* *By* J. Lockhart Clarke, *Esq.* *Communicated by* Samuel Solly, *Esq., F.R.S.*

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WHEN I had the honour of laying before the Royal Society my former researches on the structure of the spinal chord, I intimated an intention of preparing another communication on the structure of the medulla oblongata and cerebellum; but as many important points in the minute anatomy of the chord still remained in obscurity, I thought it advisable to make them first the subject of special inquiry, as far as the new method I employed would enable me to proceed. Moreover, as all investigations into the structure of any organ have, or ought to have, for their object a clearer and better knowledge of its functions, I have undertaken also to communicate in this paper whatever physiological deductions may appear to follow from my observations. Having no particular theory to support, and being influenced in these inquiries by no other feeling than the simple desire to elicit truth, the greatest care has been taken to verify my facts, and caution has been exercised in drawing conclusions from them.

It is a question of great interest and physiological importance, whether the roots of the spinal nerves belong exclusively to the spinal chord, or whether part of them ascend within either the white or the grey columns, and form the channels by which impressions are transmitted to and from the brain. On account of its interest and importance, I have employed much time and labour in endeavouring to arrive at some well-grounded and settled conclusion on this very difficult subject, having devoted to it alone many hours daily for nearly five months. So extremely intricate, however, is the internal structure of the chord; so numerous are the planes in which the nerve-roots enter the grey substance; and so various are the directions which they pursue within it, that notwithstanding the perfect transparency of my preparations, and the sharp outline which their fibres retain, my efforts to determine the exact relation between these roots and the white and grey columns appeared for some time almost hopeless; but by varying my dissections according to the exigencies of each case of difficulty, I succeeded in arriving at several results which I believe will be considered important.

That part of the fibres composing the anterior and posterior roots of the spinal nerves ascend longitudinally with the white columns, without entering the grey substance of the chord, and transmit to and from the brain impressions which give rise

to sensation and voluntary motion, is the opinion maintained by many eminent physiologists and excellent observers.

In support of this doctrine, Mr. GRAINGER*, Mr. SOLLY†, and Dr. J. BUDGE‡ have adduced the fact of having *traced* these fibres in the spinal chord of the vertebrata. A similar fact is said to have been established by Mr. NEWPORT§ and Dr. CARPENTER in the invertebrata. On the other hand, the opinion that all the fibres of the spinal nerves enter the grey substance and belong exclusively to the spinal chord, is held by TODD and BOWMAN ||, STILLING¶, VOLKMANN** and others.

In making the preparations for the investigation of this subject, I employed the second method described in my former communication on the Spinal Chord††. The animals selected for this purpose were the Ox, Calf, Cat, Rat, Mouse, and Frog. After many fruitless attempts I succeeded in rendering perfectly transparent the entire chords of the Mouse and Frog, but found that their cylindrical form interfered considerably with a distinct view of their several parts, and rendered the examination unsatisfactory. Having succeeded, however, in a similar way, with longitudinal sections of the spinal chord of the Cat, of at least $\frac{1}{12}$th of an inch in thickness and 2 inches in length, with the anterior and posterior roots attached, I was delighted, on examining these sections, with a view of its internal structure which far surpassed any I had hitherto been able to obtain.

On a former occasion, I showed unequivocally, that to the posterior white columns the posterior roots, and to the anterior white columns the anterior roots, of the spinal nerves are exclusively attached; while the lateral columns to which both these roots were formerly supposed to be connected, are in immediate connection only with the spinal-accessory nerve‡‡.

Of the Posterior Roots.—Plate XXIII. exactly represents a longitudinal section through the cervical enlargement of the spinal chord of the Cat, from the eighth to the twelfth pair of nerves. In this section the bundles which form the posterior roots P, P, P, P, are observed to consist of three kinds, which differ from each other partly in direction, and partly in the size of their component filaments.

The first kind, *a*, *a*, *a*, *a*, enter the chord transversely, and pursue a very remarkable course. I have not seen them distinctly below the cervical enlargement. Each bundle, after traversing the longitudinal fibres of the posterior columns P, C, in a compact form, and at right angles, continues in the same direction to a considerable but variable depth within the grey substance G, dilating and again contracting, so as to assume a fusiform appearance. It then bends round upon itself, at a right or more obtuse angle, and running for a considerable distance in a longitudinal direction

* Spinal Chord. † Human Brain. ‡ MÜLLER's Archiv, 1844. § Philosophical Transactions, 1843.
|| Physiological Anatomy, vol. i. 1845. ¶ Untersuchungen über die Textur des Rückenmarks, 1842.
** Nervenphysiologie, in WAGNER. †† Philosophical Transactions, 1851, p. 608, Part II.
‡‡ Many of my preparations are in the possession of the Microscopical Society of London, and the Royal College of Surgeons.

down the chord, sends forwards, at short intervals, into the anterior grey substance, a series of fibres like those issuing from the roots of plants. In this longitudinal course it is joined by corresponding fibres from bundles above and below it, which thus contribute to form a continuous band.

The fibres projecting from this band into the anterior grey substance have the following distribution. Part of them form loops with each other within the grey substance, particularly near its border; others extend directly into the anterior white columns A, C, and bending round both *upwards* and *downwards*, are seen sometimes to re-enter the grey substance and form with each other a series of loops, and sometimes to continue a longitudinal course within the anterior white columns, amongst the fibres of which they become lost. Whether the latter, also, ultimately form broader loops with corresponding fibres from the grey substance, it is impossible to ascertain. But even if those which *ascend* in the anterior columns are continued upwards to the brain, one can scarcely avoid inferring that those which *descend* re-enter the grey substance, either to form loops, or to become continuous with the fibres of the anterior roots, since the whole of the latter, as we shall presently see, proceed directly to the grey substance. Indeed, I have sometimes felt almost persuaded that a great number of the fibres of these posterior roots are directly continuous, in the grey substance, with those of the anterior roots; but I cannot make this statement with absolute certainty; and as the question is one of extreme difficulty, I shall hereafter endeavour to make it a subject of special attention.

The second kind of bundles which form the posterior roots *b*, *b*, *b*, Plates XXIII. and XXIV. traverse the posterior columns transversely, and with different degrees of obliquity from without inwards, extending nearly as far as the posterior median fissure: see also Philosophical Transactions, 1851, Plate XXIII. fig. 14. Their component filaments are finer than those of the other kind of bundles, measuring, in a recent state, about the $\frac{1}{7000}$th of an inch in diameter. They enter and pass through the posterior grey substance at various angles, and in compact bundles which decussate and interlace each other in the most complicated manner. Some of their fibres cross over to the opposite side, through the posterior commissure, behind the spinal canal; others extend into the posterior and lateral white columns; and the rest may be traced deeply into the anterior grey substance, where they separate in various directions, and are ultimately lost to view.

The bundles which compose the third kind of posterior roots enter the chord obliquely, *c*, *c*, *c*, Plates I. and II. A few of their fibres proceed near the surface both upwards and downwards, and pass out again with the roots above and below them. The rest cross the posterior white columns obliquely, and chiefly *upwards*, a small number only passing downwards. Interlacing at the same time with each other and the roots already described, they diverge, and for the most part reach the grey substance at points successively more distant from their entrance in proportion to the obliquity of their course; the remainder or most divergent taking a longitu-

dinal course with the fibres of the posterior white columns, amongst which they are lost. It is impossible to say whether any of these longitudinal fibres are continued as far as the brain, or whether they ultimately reach the grey substance of the chord. It is also extremely difficult to trace the other fibres of these roots after they have reached the posterior grey substance. In some of my finest preparations, however, they may be seen to interlace each other in a kind of network: see Plate XXIV. A large proportion diverge abruptly in various directions, so that in any section they are always divided. Many of them, both singly and in small bundles, may be observed to form loops by returning to the white columns.

Of the Anterior Roots.—The anterior roots of the spinal nerves, as I formerly described them, traverse the anterior part of the antero-lateral columns in distinct and nearly straight bundles, Plates XXIII. and XXIV. A, A, A, A. They form no interlacement with each other, like the posterior roots, until they reach the grey substance. Here their fibres diverge in every direction, like the expanded hairs of a brush. Some, near the margin, are easily seen to form loops with those of contiguous bundles; others run outwards to the lateral columns, and inwards to the anterior columns after decussating in the anterior commissure with corresponding fibres from the opposite side. A large number diverge equally *downwards* and *upwards* for some distance in the grey substance, while the remainder pass more deeply backwards and are lost. In no single instance have I seen any portion of these roots take a longitudinal course on directly entering the anterior white columns.

But besides the transverse bundles which form the anterior roots, a continuous system of exceedingly fine transverse fibres may be seen to issue from the anterior grey substance. They pass through, nearly all at right angles to, the anterior white columns, and disappear as they proceed towards the surface of the chord; but as many of them may be observed to turn round and take a longitudinal direction, it is probable that at the points where they disappear they all follow the same course. Within the grey substance they wind about and are gradually lost, mingling with the fibres of the anterior roots, and with those proceeding from the fine bundles of the posterior roots, which, perhaps, are continuous with them.

It may then, I think, be fairly laid down as a well-established fact, that nearly all, if not the whole of, the fibres composing the roots of the spinal nerves, after passing through the anterior and posterior white columns of the chord, proceed at once to its grey substance; and that if any of them ascend *directly* to the brain, it must be *those only* of the *posterior* roots which run longitudinally in the posterior columns.

That many excellent observers, with inferior means of observation, have arrived at a different conclusion on this extremely difficult subject, is not at all surprising. The opinions of Mr. GRAINGER are expressed in the following quotations from his excellent work on the spinal chord:—"After the *two* roots have perforated the theca vertebralis, and so reached the surface of the chord, it is well known that their fibres begin to separate from each other; of these fibres some are lost in the white

substance, whilst others, entering more deeply into the lateral furrows, are found to continue their course, nearly at right angles with the spinal chord itself, as far as the grey substance, in which they are lost. . . . . In examining the roots of the nerves, I have always relied on the assistance of the naked eye only, avoiding, for fear of deception, the use of a lens. . . . . From careful dissection, I am convinced that it is only a part of the fibres belonging to the *two* roots which are attached to the grey substance, and that a considerable number of threads are lost in the fibrous part of the chord. . . . . The exact mode of their connection, however, with this latter substance is not known." Only a part, therefore, of Mr. GRAINGER's statements is really correct; for though some of the fibres of the posterior roots may be confined in their course within the white columns, this is certainly not the case with regard to the anterior roots; and many of the fibres of the *posterior* roots, which appeared to him to be longitudinal, were probably those which take a very oblique course towards the grey substance. The fibres, also, of the third pair of cerebral nerves, of which some have been said by Mr. GRAINGER to be continuous with the white columns, may be all traced to the vesicular substance situated below the iter a tertio ad quartum ventriculum. Great merit, however, is due to Mr. GRAINGER for having made out so much with so little assistance.

The question, then, arises,—Do the fibres of the posterior roots which ascend longitudinally in the posterior fasciculi transmit impressions to the sensorium? In answer to this question it may be stated,—1st, that, even if they reach the brain, their number appears insufficient to convey such impressions from all parts of the body; and 2ndly, that the anatomical connection of the posterior columns exclusively with the cerebellum would, *à priori,* lead us to a negative conclusion, unless we regard this latter organ as the common centre of sensation, which we have no grounds for believing it to be. But the same anatomical connection of the posterior columns with the cerebellum clearly indicates that they establish *some* physiological relation between this organ and the spinal chord; and if the cerebellum were proved to be, according to the generally received opinion, a centre of *motor* power *only*, destined for the control and coordination of complex muscular movements, it would follow that these columns were motor, and not sensitive, whether or not we admit them to be constituted wholly, or in part, of the longitudinal fibres of the posterior roots*.

Upon anatomical grounds, then, it would appear, that the posterior white columns are not the channels of communication between the sensorium and the posterior spinal nerves. Experimental evidence tends to the same conclusion. Both VAN DEEN† and STILLING found that irritation of these columns excited no sensation

* That the cerebellum is in *some way* concerned in the regulation and coordination of muscular movements appears to follow from experiment and pathological investigation; but I think there are reasons for believing that the *mode of action* usually assigned to it is unsatisfactory, and at variance with many well-established facts. The discussion of this question, however, would be foreign to the present subject.

† Traités et Découvertes sur la Physiologie de la Moëlle Epinière. Leide, 1841.

when their connection with the grey substance was interrupted. Nothing, however, is more certain than that the posterior roots are in *immediate* connection exclusively with these columns, which are separated from the antero-lateral columns by the posterior lateral fissure, through which a few only of the roots proceed to the grey substance. It is difficult, therefore, to conceive how sensory impressions can be conveyed after destruction of the posterior columns, as *appears* to have taken place in cases put on record by several observers. The only explanation of which these cases seem to admit, is that either these columns were only partially destroyed, or that sensory fibres are contained also in the anterior roots.

The question, then, remains,—By what means *are* impressions which are received by the chord transmitted upwards to the brain?

By Volkmann it is believed that all, or nearly all the fibres of the nerve-roots terminate in the grey substance of the chord. In support of this opinion, he endeavours to show, both by measurement and weight, that there is no progressive increase, from below upwards, in the size of the white columns; that, on the contrary, he found these columns absolutely smaller in the cervical region than in the lower parts, and everywhere in direct proportion to the quantity of the grey substance. He further states, that the total area of all the spinal nerves cut transversely is many times greater than the area of a transverse section of the chord above the first cervical nerve. Opposed to that of Volkmann is the opinion of Kölliker*, who holds that the white columns of the chord are composed entirely of fibres derived from the spinal nerves. This opinion is founded on the fact pointed out by him,—and about the same time by myself,—that at least a large proportion of both roots, after passing through various parts of the grey substance, pursue a longitudinal course within the white columns. He further maintains, in opposition to Volkmann, that these columns do really increase progressively towards the brain, and that the nerve-fibres of which they mainly consist, do not recover their original diameter which they lost in passing through the grey substance. From these facts he calculates that the white columns are sufficiently large in the cervical region to give passage to all the spinal nerves, and that they form the channels of communication to and from the brain.

The results of my own observations are opposed to those of Volkmann, and partly in favour of those of Kölliker. In all the Mammalia examined by myself, I have found the quantity of the white substance of the chord absolutely greater in the cervical region than elsewhere. It cannot therefore be, as stated by Volkmann, in direct proportion to the grey substance, since the latter is far more abundant in the lumbar enlargement. Again, his opinion that all, or nearly all the spinal nerves terminate in the grey substance of the chord, is refuted by the fact, shown by both Kölliker and myself, that at least a great number of them do really pass out of the grey substance as longitudinal fibres of the white columns. But on the other hand,

* Mikroskopische Anatomie, Band ii.

I cannot agree with the statement of KÖLLIKER, that all these fibres continue the same course within these columns in the direction of the brain; for it is certain, as I have already observed, that many of them not only pursue a *descending* course, but that others which actually *ascend* re-enter the grey substance to form loops. It is certain, also, that of the anterior roots in particular, the fibres, on reaching the grey substance, diverge in a direction as much *downwards* as upwards.

It seems therefore that many of the fibres which belong respectively to the anterior and posterior roots, in different regions of the chord, terminate there by forming with each other a series of loops, partly within the grey substance, and partly after extending through the latter into the white columns; and that these loops are of various sizes and lengths. Nor is it improbable that some of them may reach even as far as the brain, since it is well known that the formation of loops is at least one mode in which nerve-fibres terminate there. I am far from denying, however, that a portion of the roots may be connected with the vesicles of the chord.

Does the *grey substance* of the chord transmit impressions to and from the brain?—STILLING divided, in a living animal, the anterior white columns through their whole thickness, and found that voluntary power was still conveyed to parts below the section; but when the incision extended deeply into the grey substance, all voluntary movements were interrupted. From this experiment he infers that the grey substance alone is the conductor of voluntary power from the brain to the anterior roots; and the means of communication he explains by a system of fine longitudinal fibres which he found in the anterior grey substance. I thought formerly that I also had seen such fibres in comparatively small numbers; but further and more careful observation has led me to the conclusion, that excepting those in the *substantia gelatinosa* and those near the border of the *substantia spongiosa*, there is no regular system of fine longitudinal fibres in the grey substance. In looking for such fibres I have always selected a perfectly fresh chord. An exceedingly thin section, which by practice may be made with a very sharp instrument, was carefully laid on a glass slide and treated with acetic acid, which increases its transparency without producing any material alteration in the appearance of its fibres. It was then covered with thin glass, and examined, without any pressure, under sufficiently high powers. In such a section, fibres of various diameters—many exceedingly fine—may be seen to cross each other in every direction, but not in one direction more than another. It is probable that even the longitudinal fibres of the *substantia gelatinosa* are not continued, *individually*, as far as the brain, but pass out at intervals into the white columns, since their number, as well as the breadth of the *substantia gelatinosa*, does not increase regularly from below upwards. I believe that they are all derived from the fine bundles of the posterior roots*.

* KÖLLIKER supposes that the nucleated fibres of the *substantia gelatinosa*, described by REMAK, are processes of the nerve-vesicles; but these processes contain no nuclei. It is more probable that the fibres of REMAK are really small blood-vessels, which have precisely the same appearance, and of which a large number enter with the posterior roots and pursue the same longitudinal course in the *substantia gelatinosa*.

The results obtained from the experiments of STILLING above described are involved in much obscurity; for in addition to other reasons, it would seem extremely difficult, if not impossible, to avoid leaving a portion of the anterior columns undivided,—that portion, namely, which is situated internal to the anterior grey substance. But even if they tended to show that the power of volition is not transmitted by these columns, they by no means prove it to be communicated by the grey substance, since a deep incision into the latter would divide not only many fibres of the anterior roots extending upwards, but a portion also of the lateral white columns into which these roots are prolonged.

That the grey substance of the chord does transmit impressions *from one side to the other, has been* fully proved by the experiments of VAN DEEN and STILLING; and the means by which the communication is effected is satisfactorily explained by the structure of the transverse commissure described by both STILLING and myself*. I believe, however, that the fibres of this commissure do not form a distinct set connecting the grey substance of one side with that of the other, but that they are all continuous with the roots of the nerves and the white columns†.

From certain facts, then, described in this communication, it would appear that the white columns are mainly constituted of fibres derived from both roots of the nerves. It is true that the processes of some of the vesicles situated near the margin of the grey substance may be seen to extend into these columns, with fibres of which they perhaps are continuous; and it is not improbable that others more deeply seated may have the same connection. But if there be, as some physiologists believe, a

* The structure immediately surrounding the spinal canal is described by STILLING as a *circular commissure* composed of fine grey fibres. By REMAK it is spoken of as the *commissura gelatinosa*, and as a continuation of the *substantia gelatinosa* of the posterior grey substance. KÖLLIKER, who declares that this structure was mistaken by STILLING for a spinal canal—the existence of which he denies—also considers it as a peculiar kind of vesicular substance, enclosing a central nucleus, (*grauer centraler Kern*) and which he calls the *substantia grisea centralis*. It appears, however, as described in my former communication, to consist of a circular layer of fine fibrous tissue surrounding and supporting the columnar epithelium which forms the wall of the spinal canal. The existence of this canal is unquestionable; but in the human chord it is often closed, and reduced, as if by lateral pressure, to a mere line; and around this the columnar epithelium is arranged in the form of an ellipse, which KÖLLIKER appears to have mistaken for a double nucleus.

† There seems to be a great correspondence in the fibrous arrangement between the grey substance of the spinal chord and the chiasma of the optic nerves. In a few transparent preparations that I have made of the latter:, the structure first pointed out by MAYO is very clearly discerned; but the course of the fibres is found to be still more intricate. There is a remarkable circumstance that I have observed, and which I do not recollect to have seen recorded, respecting the cross action of the optic nerves. After looking through the microscope, if the eye employed be directed to other objects, it must be well known that the *definition* is found to be unimpaired, although the *colour* is rendered darker than natural, in direct proportion to the previous stimulus of light; but if the same objects be viewed by the other eye which has not been employed at the microscope, I have invariably noticed that an opposite effect is produced, and in the same proportion,—the *colour* remains *natural*, but the *definition* is more or less *impaired*. It may be stated then as a law, that, *By close observation with magnifying glasses, under the stimulus of a strong light,—in the eye employed, the perception of colour, but not the defining power, is affected; while in the opposite eye, the defining power, but not the perception of colour, is impaired, and in a direct and equal ratio.*

direct continuity between the cerebral fibres and the caudate vesicles of the chord, I am disposed to think it is established by means of the system of fine nerve-tubes which are seen to proceed from the grey substance of the latter as longitudinal fibres of the white columns. In opposition to WAGNER, I agree with KÖLLIKER in the opinion that the process of a nerve-vesicle never becomes the axis-cylinder of a double-contoured nerve-tube, and that what WAGNER considered as the process of a nerve-vesicle was probably the axis-cylinder itself. The evidence of any direct connection between these processes and the roots of the nerves is very unsatisfactory; for amongst thousands of preparations examined by myself with the greatest care, I met with a few cases only in which it was at all probable.

If any of those fibres of the posterior roots, which, after traversing the grey substance, enter the anterior white columns, could be proved to extend as far as the brain, the indications of sensation which are said to have followed irritation of these columns might be thus explained. It is quite certain, however, as already stated, that an equal number of those fibres pursue a *downward* course. On the other hand, if the anterior columns really be, as I believe they are, one of the channels which transmit downwards the influence of the will, they can perform this office only by first entering the grey substance, since into this all the fibres of the anterior roots may be traced. The same inference may be drawn with regard to the lateral white columns, which from their connection, through the grey substance, with the roots of the nerves, would appear to be both sensitive and motor.

The fact that many fibres of each root, on entering the grey substance, not only extend both upwards and downwards to a considerable distance beyond their point of entrance, but intermingle also in the most intricate manner with those of other roots, may serve to explain how impressions made at one particular spot are communicated in different directions to distant parts of the chord, so as to excite a simultaneous and sympathetic action in classes of muscles which otherwise would appear unconnected. It is probable that the fibres which quit the grey substance and return to it by the formation of loops within the white columns, may take that course for the purpose of stimulating particular parts of that substance, without affecting those which are intermediate.

In concluding this series of investigations, it has appeared to me, that, considering the beauty and transparency of my preparations, the distinctness with which their several parts are preserved, and the persevering labour which has been bestowed upon them, I might almost venture to think we have obtained nearly all that it is possible to know—with our present means—concerning the minute anatomy of the spinal chord. Our further progress is arrested chiefly by the continual and intricate deviations observed in the course of its fibres, and the consequent disorder in which its elements appear to be involved, when viewed in section. The confusion, however, is doubtless only apparent; for in this wonderful organ, with all its complexity of structure, we have no reason to doubt the constant and uniform existence of that

beautiful order and design so conspicuously manifested by organic life in the formation of every part which science has revealed to the inquiring eye. Every fibre, probably, has its own fixed and appointed course, in accordance with the particular function it is destined to perform.

Explanation of the Plates.

PLATE XXIII.

Represents a longitudinal section through the cervical enlargement of the spinal chord of the Cat, from the 8th to the 12th pair of nerves. Magnified 30 diameters*.

P, C. Posterior white columns. A, C. Anterior white columns. G. Grey substance between the white columns. P. Posterior roots of the nerves, consisting of three kinds,—*a*, *b* and *c*. The second kind, *b*, traverse the posterior columns at first obliquely towards the mesial line, that is, in a plane oblique to that of the section, and were therefore divided near the surface of the chord. A. Anterior roots of the nerves. A, C′. A portion of the anterior column, showing the arrangement of their longitudinal fibres.

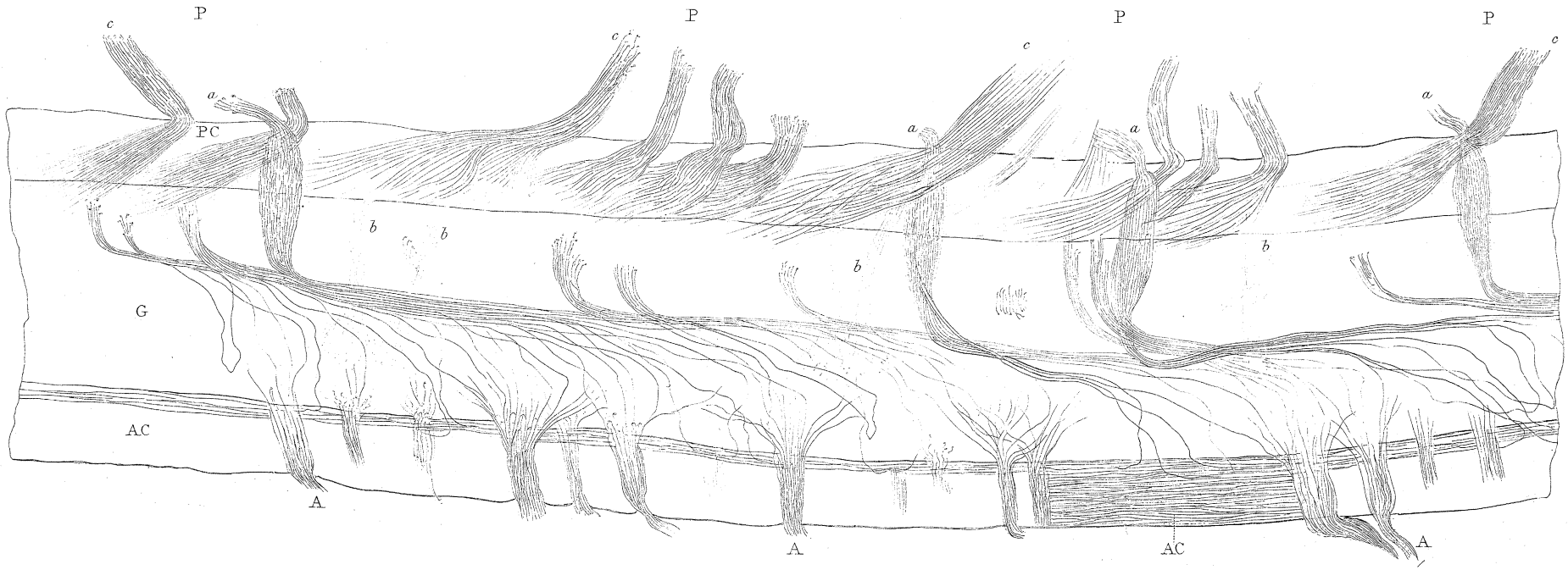
PLATE XXIV.

Represents a longitudinal section through the lumbar enlargement of the spinal chord of the Ox. Magnified 30 diameters.

P, C. Posterior columns, showing the intricate interlacement formed by the posterior roots of the nerves. P. Posterior roots. A, C. Anterior white columns. A. Anterior roots of the nerves. G. The anterior and posterior grey substance traversed by the fibres of the anterior and posterior roots of the nerves. *g*. The *substantia gelatinosa*.

In both Plates the vesicles have been omitted in order to avoid obscuring the fibres, which were observed by means of Ross's half-inch object-glass, with No. 2 eye-piece, giving a power of 150 diameters.

* The outlines of the drawings were made by means of a power of 40 diameters, but were reduced nearly one-third by the engraver.



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Drawn by J. L. Clarke, from nature.

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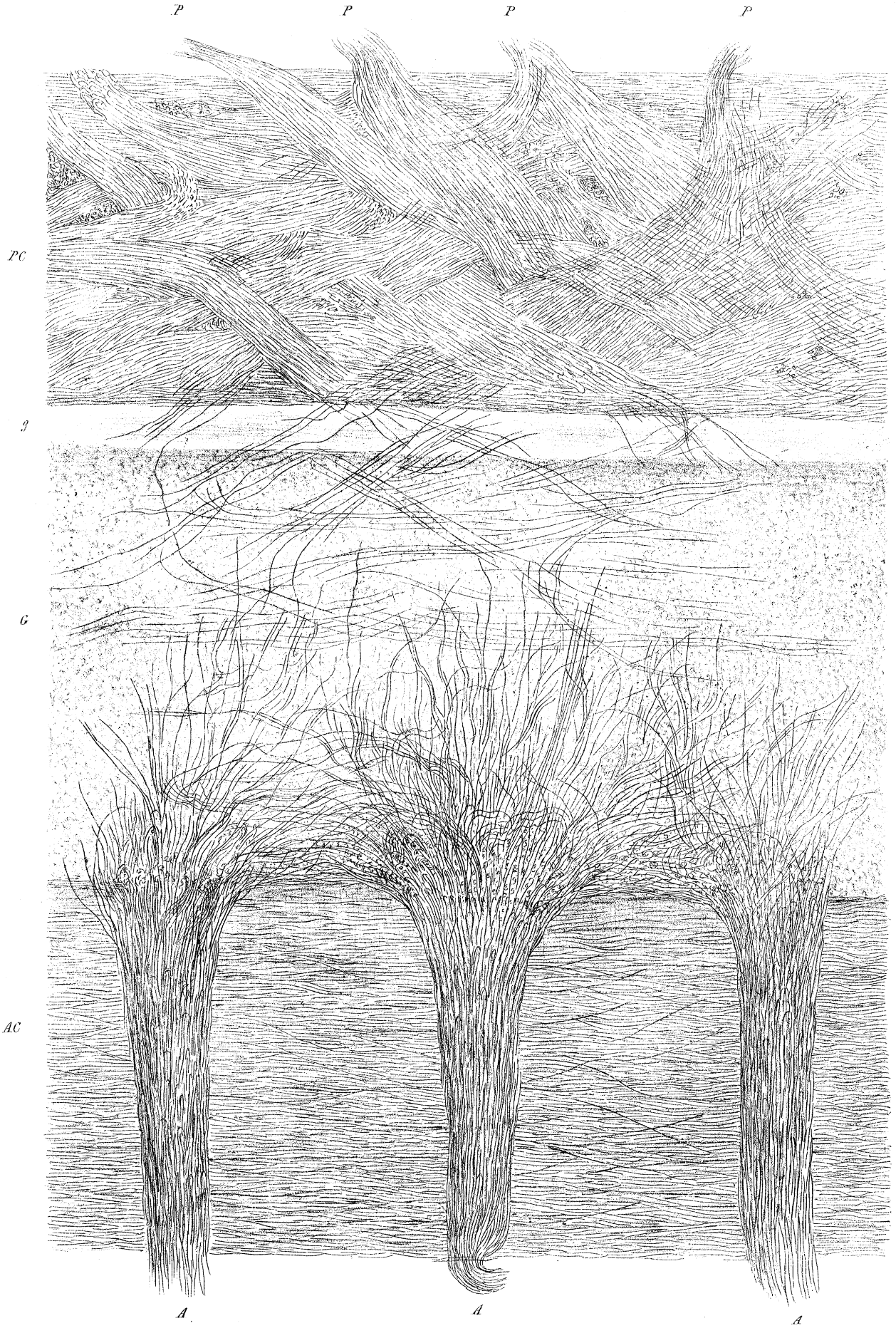

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Drawn by J.L. Clarke from Nature.

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