

THE RAMI COMMUNICANTES IN THE RHESUS MONKEY

BY D. SHEEHAN AND J. PICK

Department of Anatomy, New York University College of Medicine

In a recent study of the small myelinated fibres in ventral spinal roots (Sheehan, 1941) the limits of the thoraco-lumbar outflow in the monkey were defined as T1/T2-L3/L4, rarely L5, and in man as T1-L2. The observations fitted into the general pattern of the sympathetic system, described first in the dog and cat by Gaskell (1886) and Langley (1894). In the rami communicantes, however, the small medullated fibres are distributed more widely. Not only do they take part in the constitution of the white rami of the thoraco-lumbar region, but they are also found in almost all the grey rami, particularly in those of the lower cervical and lower lumbar nerves. Langley (1896) was well aware of their existence within grey rami; the term 'grey', he remarked, is one of convenience rather than of anatomical accuracy. Kiss & Mihálik (1929) go so far as to deny any basic histological distinction between grey and white rami. Mixed rami are so common that, in their opinion, a pure grey or a pure white ramus is rarely seen. There are obviously widely possible differences in the interpretation of the microscopical appearances of sympathetic rami. Thus the number of myelinated fibres found in the rami of L3 and L4 led Müller (1909) to conclude that the thoraco-lumbar outflow extended in man as far down as the fourth lumbar segment. Further, a white ramus connected with the eighth cervical nerve has been mentioned as an occasional finding by Harman (1900) and Wrete (1934), and yet, in all examples that have been examined, its ventral spinal root is virtually devoid of the small myelinated fibres of the size constituting the thoraco-lumbar outflow.

What then are the criteria by which we distinguish a white ramus? Are the white rami distributed strictly within a thoraco-lumbar outflow as defined by a study of the ventral spinal roots? And what is the significance of the small myelinated fibres within rami, admittedly grey, and lying outside these limits? Langley (1896) and Nevin (1930) believed that the majority were postganglionic in nature, but Ranson & Billingsley (1918) and Kuntz & Farnsworth (1931) showed that some were afferent, at least with a cell station lying within dorsal spinal roots. That others, though a minority, might be preganglionic fibres passing to aberrant sympathetic nerve cells lying along grey rami or within spinal nerve roots, was first suggested by Langley (1896), and the hypothesis has recently been elaborated by Wrete (1935).

With these questions in mind we have undertaken a full histological investigation of the sympathetic rami in the monkey, in order to obtain a basis for comparison with the study of the ventral roots, already reported. There has apparently been no previous communication on the fibre constitution of the rami in the macaque. Gross anatomical studies have been undertaken by Broeck (1907-8) and by Botár (1932) in single examples of various species of monkey. In the rhesus monkey, dissections have been made of the cervical sympathetic chain by Riegele (1926), of the lumbo-sacral portion by Trumble (1933-4) and of the coccygeal region by Schumacher (1905), but by far the most complete study of the distribution of the rami communicantes in the macaque has been carried out by Zuckerman (1938), and the details of gross anatomy which

are reported incidentally in the present paper serve merely to supplement these earlier observations. A general account of the autonomic nervous system in the rhesus monkey by Kuntz (1933) is to be found in the monograph on the anatomy of this animal. No statistical data on the commoner variations have been reported.

The surgical importance of defining accurately the distribution of the white rami communicantes is of special significance to-day when a preganglionic section is being recommended as the operation of choice where sympathetic denervation of a part is desired. Should many of the small myelinated fibres in grey rami prove to be preganglionic, however, the anatomical basis for all operations on the sympathetic chain would be altered.

MATERIAL AND METHODS

The sympathetic chains together with the rami communicantes to spinal nerves have been dissected on both sides in twenty rhesus monkeys (*Macaca mulatta*). The communicating rami of the upper cervical nerves were only included in the last six preparations; otherwise the dissections were complete. The visceral and other rami were omitted as their dissection would have complicated and lengthened the study unduly. The animals had previously been used for experimental purposes and had been fixed immediately after death by intravascular injections of 10% formol-saline. The dissections were recorded by diagrams in each case.

In ten of the series, typical rami from various regions, particularly from the lower cervical and upper lumbar levels (boundaries of the thoraco-lumbar outflow), were removed and placed in 10% formol-saline for 24 hr. They were then washed and stained in bulk in 1% osmic acid, and sectioned in paraffin (5 μ thick). A certain amount of shrinkage undoubtedly occurred by this procedure, but as this applied to all fibres their relative sizes were not materially altered.

NOMENCLATURE

There are two possible methods of enumerating the ganglia in gross dissection. A ganglion might be numbered according either to the spinal nerve to which its grey ramus passed, or to that joined by its white ramus, as these terms are customarily defined. Zuckerman (1938) advocated the latter as the method of choice for embryological reasons but, in point of fact, a white ramus is not necessarily related in function to its corresponding sympathetic ganglion, for many of its fibres run through and terminate in other ganglia higher or lower in the chain. Indeed, the fibres entering the sympathetic trunk through one white ramus may be distributed to 5-10 successive ganglia. Furthermore, certain ganglia receive two and even three white rami from several spinal nerves. Enumeration of the ganglia according to the grey rami, on the other hand, seems to be more practical, since the grey ramus appears to connect a spinal nerve specifically with the ganglion of the same segment. This method was used by Langley (1896) and by Ranson & Billingsley (1918).

In the upper thoracic region the matter is simple, since the ganglia are each connected with only one spinal nerve. In the lower thoracic and upper lumbar regions, however, a ganglion is almost invariably connected with two or more spinal nerves. Botár (1932) has pointed out that the course of the white rami in the lumbar region is oblique, but in a gross dissection it is impossible without histological verification to distinguish a white from a grey ramus. In the present study, therefore, it was found necessary to lay down certain arbitrary rules, in order to bring about a uniformity in the descriptions

of the various dissections, and to permit accurate comparison when the microscopical studies were available.

Enumeration was started in each case with the ganglion connected with the third thoracic spinal nerve. This was constant and could be readily recognized. Naming this the third thoracic ganglion, enumeration followed downwards consecutively as far as the eleventh thoracic ganglion, which usually lay on the body of the twelfth thoracic vertebra. The ganglion immediately below this lay on the body of the first lumbar vertebra and was connected by rami with both the twelfth thoracic and first lumbar nerves, the former connexion subsequently proving to be the white ramus. Had the ganglia been enumerated according to the white rami, this would have been the twelfth thoracic, and the next lower ganglion would have been the first lumbar. The last lumbar and all the sacral ganglia would then have been numbered according to a spinal segment with which they had no connexion. The ganglion in question, located on the body of the first lumbar vertebra, and connected with both the twelfth thoracic and first lumbar nerves, was therefore called the first lumbar. Counting down in sequence now gave a regular enumeration of seven lumbar and three sacral ganglia. In only one monkey were thirteen ribs found, and Zuckerman's suggestion (1938) that the thirteenth thoracic nerve and its corresponding ganglion be called the first lumbar was followed; the total number of lumbar nerves then became eight as there was an extra vertebra in the thoraco-lumbar region.

At the upper end of the thoracic sympathetic chain the second thoracic nerve was either connected with the stellate ganglion or with a separate ganglion (the second thoracic). In the latter instance the stellate was formed by a fusion of the lower cervical and first thoracic ganglia only. In the other examples the second thoracic ganglion was incorporated within the stellate. Between the stellate and the superior cervical ganglion there was a small middle cervical ganglion placed invariably at the upper junction of the two limbs of the subclavian ansa.

This method of enumeration was satisfactory when a regular number of ganglia was encountered. Occasionally, however, it was obvious from the precise connexions of the rami and from the total number of ganglia present that there had been a fusion of two or more ganglia, or a splitting of one ganglion into two smaller masses. This usually occurred in the lumbo-sacral region. Such variations were taken into account in the method of enumeration, and described separately. Although considerable irregularity in the number and arrangement of the ganglia and rami existed, a definite pattern could be easily recognized, and the frequency of variation from this pattern defined.

FORM AND CONNEXIONS OF THE SYMPATHETIC CHAIN AND GANGLIA

The regular course of the sympathetic chains followed closely that outlined by Kuntz (1933) and Zuckerman (1938), and needs no further description.

Some form of transverse connexion between the sympathetic chains of each side was a constant feature in every dissection. Two types were generally recognized, one in the form of a complete fusion of the corresponding ganglia of each side, and the other as short nerve strands connecting the two chains. Both types were found present in the same dissection at different levels, the short intercommunicating branches more often in the lower lumbar and upper sacral regions, the fused ganglia more often at the termination of the two chains over the coccyx. In one instance the lumbar chains

were placed unusually close together on the ventral surface of the vertebral bodies, and fusion of the fifth lumbar ganglion of each side occurred in the midline. Transverse connexions never occurred above the level of the fourth lumbar vertebra. In the sacral region, a ganglion on one side occasionally gave a ramus to the corresponding spinal nerve of the opposite side, forming another, rather unusual, type of transverse connexion.

The sympathetic chain was rarely double, only eleven times in forty sides dissected. It occurred between the levels of the twelfth thoracic and first sacral vertebrae, and was therefore a peculiarity of the lumbar sympathetic chain. A doubled chain never extended for any greater distance than the interval between two adjacent ganglia, so that in an experimental extirpation of the lumbar chain it would not be easily overlooked.

In the more regular examples there were, according to the method of enumeration adopted here, three cervical, eleven thoracic (including those thoracic ganglia incorporated within the stellate), seven lumbar, three sacral and one or more coccygeal ganglia. The total number in any particular case might be altered in three ways: (a) by *fusion* of two adjacent ganglia, (b) by *absence* of a ganglion (revealed by the rami arising from the chain directly), and (c) by *duplication* of a ganglion. Because more than one of these conditions was frequently present, the simple recording of the total number of ganglia in any one instance has no special significance. Thus a count of twelve thoracic ganglia would not mean a special extra ganglion for the twelfth thoracic nerve, but frequently a duplication of the ninth or tenth thoracic ganglion. In the lumbar region the number of ganglia varied from six to eight, with duplication of the fourth lumbar occurring in ten instances.

Superior and middle cervical ganglia. The superior cervical ganglion was regular and placed in all instances opposite the bodies of the upper two cervical vertebrae. The upper pole could be clearly defined between the jugular and carotid foramina. Rami were traced to the upper three cervical nerves, usually only one to each nerve.* Several rami connected the superior cervical ganglion with the ninth, tenth, eleventh, and twelfth cranial nerves, and in one or two instances the separation of the ganglion from the nodose ganglion of the vagus was difficult.

The superior cervical ganglion was connected by a long thin nerve trunk, the cervical sympathetic cord, with the middle cervical ganglion, placed usually opposite the intervertebral disc between the seventh cervical and first thoracic vertebrae, and immediately above the first part of the subclavian artery. The left middle cervical ganglion was therefore generally lower than the right. The two limbs of the subclavian ansa joined the middle cervical ganglion with the stellate. Neither from the cervical sympathetic cord nor from the middle cervical ganglion were any rami communicantes traced to the cervical nerves. Communications with the vagus and its recurrent laryngeal branch were common. The constancy and regularity in position of the middle cervical ganglion in the monkey contrasted with the more variable conditions found in man (Axford, 1927-8; Siwe, 1931; Sheehan, 1933).

Stellate ganglion. In twenty-seven instances the stellate ganglion represented a fusion of the inferior cervical, first and second thoracic ganglia, and was situated opposite

* For purposes of description and before the histological preparations had been studied, the rami were referred to in the gross dissections as passing from a ganglion to a spinal nerve, realizing of course that conduction in its constituent fibres might be in the opposite direction.

the bodies of the first and second thoracic vertebrae. In twelve instances it was formed by the inferior cervical and first thoracic ganglia only, and did not extend caudally beyond the lower limits of the first thoracic vertebra. In these examples the next lower ganglion, connected with the second thoracic nerve, was clearly a separate second thoracic ganglion. In one exceptional arrangement two ganglia took the place of the

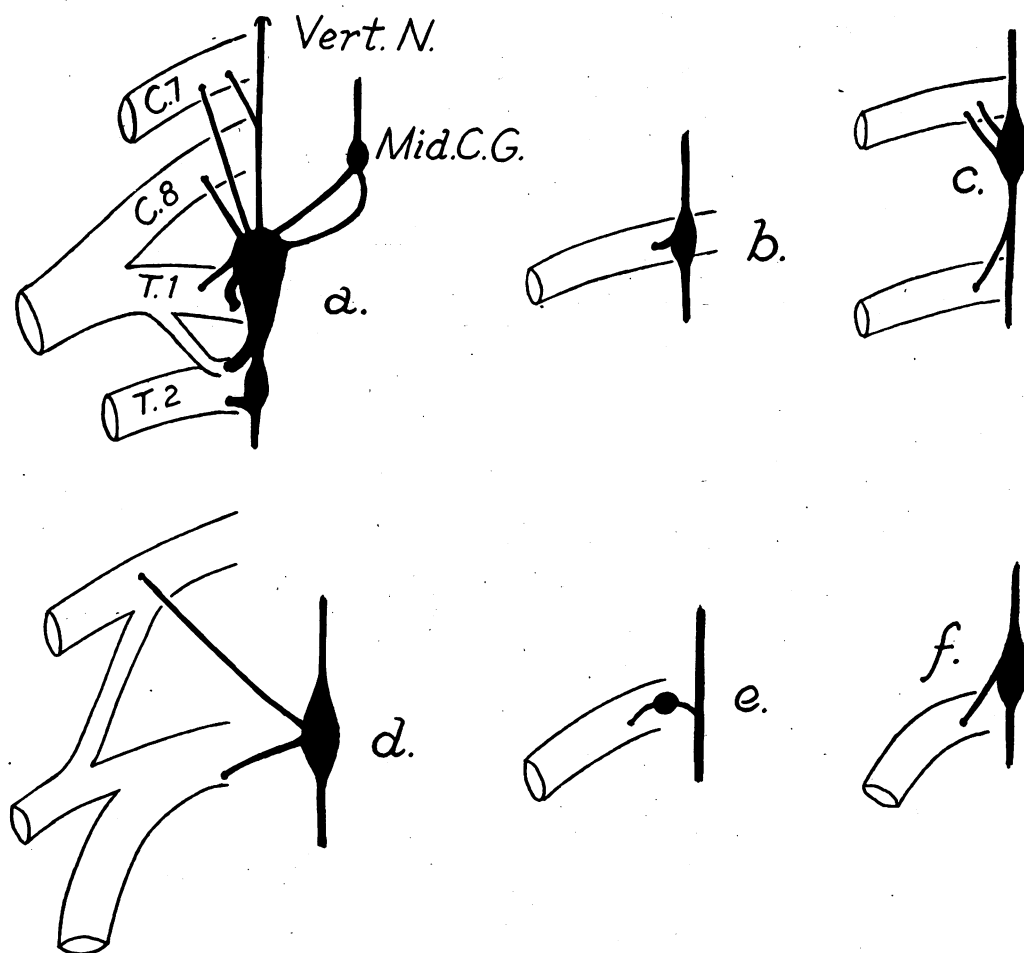


Fig. 1. Diagrammatic form of ganglia at different levels: (a) stellate; (b) upper thoracic (T3-T7); (c) lower thoracic (T8-T12); (d) upper lumbar (L1-L4); (e) intermediary ganglion on the course of a grey ramus (L2); (f) lower lumbar and sacral (L5-S3).

stellate; there was a small inferior cervical ganglion, and just below it a larger mass representing a fusion of the first and second thoracic ganglia. In the following analysis of the data concerning the rami of this region, the two ganglia in this exceptional case have been regarded as homologous with the stellate.

The communicating rami from the stellate ganglion were principally distributed to the nerves taking part in the brachial plexus (*a* in Fig. 1). They can be listed as follows:

- (1) *Vertebral nerve*, present in all instances, and from which arose:
- (a) Ramus to C8 (thirty-two out of forty instances).
 - (b) Ramus to C7 (thirty-six out of forty instances).
 - (c) Ramus to C6.
 - (d) Ramus to C5.
 - (e) Ramus to C4.

The vertebral nerve was traced through the transverse foramina of the cervical vertebrae in six dissections, and in every instance the rami to C6, C5 and C4 were present, although the last was often difficult to trace.

- (2) *Rami to C7* (in addition to those from the vertebral nerve):

None	20 instances
One ramus	17 „
Two rami	3 „
Total	40 „

- (3) *Rami to C8* (in addition to those from the vertebral nerve):

None	15 instances
One ramus	20 „
Two rami	3 „
Three rami	1 „
Four rami	1 „
Total	40 „

In those examples where no separate rami were given off to C7 or C8, the nerves invariably received a branch from the vertebral nerve (as described above).

- (4) *Rami to T1*:

One ramus	10 instances
Two rami	20 „
Three rami	10 „
Total	40 „

- (5) *Rami to T2*:

None	1 instance
One ramus	30 „
Two rami	7 „
Three rami	2 „
Total	40 „

These arose directly from the stellate in the twenty-seven instances where the second thoracic ganglion was incorporated in the fused mass. In twelve they came from a separate thoracic ganglion.

(6) *Ramus to that part of T2 which joins the brachial plexus*. This ramus was found in ten of the forty instances. It arose invariably from the stellate ganglion, irrespective of whether or not a second thoracic ganglion existed. It was a short thick ramus and joined the portion of the second thoracic nerve in such a manner that the latter often appeared to be its continuation. Indeed it was not always clear whether there existed

a true contribution from T2 to the brachial plexus, or merely a rather thick sympathetic ramus passing up to the first thoracic nerve.

Upper thoracic ganglia (T2-T7). The third to the seventh thoracic ganglia, and the second thoracic when separate, presented a uniform pattern (*b* in Fig. 1). Each ganglion was small and placed opposite the lower border of its corresponding vertebral body or more often the succeeding intervertebral disc. Fusion of two adjacent ganglia or duplication of a ganglion occurred rarely. Each ganglion was connected simply by one or more rami with its corresponding spinal nerve. A single ramus was the rule. Individual variations are listed in Table 1.

Lower thoracic ganglia (T8-T11). The lower thoracic ganglia represented a transition from the simple form of the higher thoracic ganglia to the more complex arrangement in the upper lumbar region. Slightly larger than the preceding ganglia, they are placed opposite the corresponding intervertebral disc or the next lower vertebral body. The relative position of the ganglion to the corresponding nerve was therefore lower and the rami consequently became more oblique (*c* in Fig. 1). Fusion and duplication were common. Each ganglion was connected, usually by two rami, with its corresponding spinal nerve, and in addition in some instances by a ramus with the spinal nerve of the next lower segment. This increasing tendency of a ganglion to connect with two spinal nerves instead of one was an almost constant feature of the eleventh thoracic ganglion and was the standard pattern in the upper lumbar region. Individual variations are summarized in Table 1.

Upper lumbar ganglia (L1-L4). These ganglia were the largest in the entire chain and were placed opposite the bodies of the corresponding vertebrae. Some form of fusion or of duplication was almost the rule in some part of this region. Each ganglion was connected by one or more transverse rami with its corresponding spinal nerve, and by an oblique ramus with the spinal nerve preceding, in some instances with a spinal nerve two segments higher (*d* in Fig. 1). The oblique ramus left the spinal nerve where it was entering into the formation of the lumbar plexus, therefore at a point unusually distal as compared with other levels. Zuckerman (1938) has noted this particularly in relation to the genito-femoral nerve. As the oblique connexions proved subsequently to be white rami, preganglionic fibres must travel considerable distances in the spinal nerve before emerging in the white ramus (*b* in Fig. 3). Often a ramus bifurcated so as to join two spinal nerves and conversely, two rami, each from a separate ganglion, frequently united to pass to one spinal nerve. The individual variations encountered were many, as will be seen from Table 1. Where a ganglion was connected with only one nerve, the other nerve usually received a ramus directly from the sympathetic cord either above or below the ganglion. In three instances the second lumbar ganglion was represented only by a small mass situated along the course of the grey ramus to L2 (*e* in Fig. 1).

Lower lumbar, sacral and coccygeal ganglia (L5-Cocc.). The form and connexions of these lower ganglia demonstrated a gradual 'return' to the pattern observed in the upper thoracic region, namely a smaller ganglion connected by one descending ramus, rarely two, with its corresponding nerve (*f* in Fig. 1). Duplication was rare, but absence of a ganglion, particularly in the lower sacral region, was common. There was always some form of fusion of the terminal parts of the sympathetic chains of each side, over the lower sacrum or upper coccyx, but sometimes this mid-line fusion occurred higher, once as high as the fifth lumbar. Individual variations are listed in

Table 1. In one monkey with 13 ribs there was an extra thoraco-lumbar vertebra, which was called the eighth lumbar. Thus in two dissections (right and left sides) there was an eighth lumbar ganglion, with connexions on the right side with L7, L8 and S1, and on the left with L8 and S1 spinal nerves. On the right side of this animal the seventh lumbar ganglion was absent, and it is possible that the ganglion lying on the body of the eighth lumbar vertebra might have been a fused seventh and eighth lumbar. The coccygeal ganglia, minute in size, single or multiple, were almost invariably fused in the mid-line on the ventral surface of the coccyx, and gave a fine ramus on each side to the coccygeal nerves. The rami were extremely difficult to trace and variations observed were uncertain; for this reason they have been omitted from Table 1.

From the interganglionic parts of the sympathetic chain below the eighth thoracic level, rami were found joining the spinal nerves. They occurred most frequently between the eleventh thoracic and the third lumbar levels. In the sacral region such rami were associated with a missing ganglion, but elsewhere they were generally additional to the usual ganglionic rami, which might in such a case be reduced in number. The percentage frequency with which each spinal nerve received one or more rami communicantes is listed in Table 2.

Table 2. *Percentage frequency (nearest whole number) with which each spinal nerve receives one or more communicantes (rhesus monkey)*

Spinal nerve	Rami communicantes							
	None	One	Two	Three	Four	Five	Six	Seven
T1	—	28	45	27	—	—	—	—
T2	—	55	40	5	—	—	—	—
T3	—	98	2	—	—	—	—	—
T4	—	90	10	—	—	—	—	—
T5	—	78	22	—	—	—	—	—
T6	—	63	37	—	—	—	—	—
T7	—	63	35	2	—	—	—	—
T8	—	43	57	—	—	—	—	—
T9	—	18	75	7	—	—	—	—
T10	—	8	75	12	5	—	—	—
T11	3	20	67	10	—	—	—	—
T12	—	5	75	20	—	—	—	—
L1	—	8	55	35	2	—	—	—
L2	—	3	47	37	10	3	—	—
L3	—	—	25	35	28	8	2	2
L4	—	28	52	20	—	—	—	—
L5	—	73	27	—	—	—	—	—
L6	—	65	30	5	—	—	—	—
L7	—	40	55	3	2	—	—	—
S1	3	85	10	2	—	—	—	—
S2	13	77	10	—	—	—	—	—
S3	13	87	—	—	—	—	—	—
Cocc. 1	18	82	—	—	—	—	—	—

CONSTITUTION OF THE RAMI

It became evident from the histological studies of the rami that a simple classification into grey and white could not be followed. Instead, four general types came to be recognized (Fig. 2) and these have been designated as follows:

Type 1 consisted of myelinated fibres of all sizes, ranging up to 15μ in diameter. The small fibres (3μ and less) by no means dominated the picture. There was a fairly equal distribution of the various size groups, scattered irregularly throughout the

ramus, giving an appearance of lack of uniformity. This is evidently the white ramus as described by Gaskell and Langley. It was very distinct when present, and was sharply differentiated from the other types.

Type 2A consisted almost entirely of non-myelinated fibres, with often a fine scattering of small medullated fibres (under 3μ in diameter) totalling not more than fifty odd in any single ramus. They were 'sprinkled' fairly uniformly throughout the section. Occasionally, and this was particularly true of the cervical rami, there was

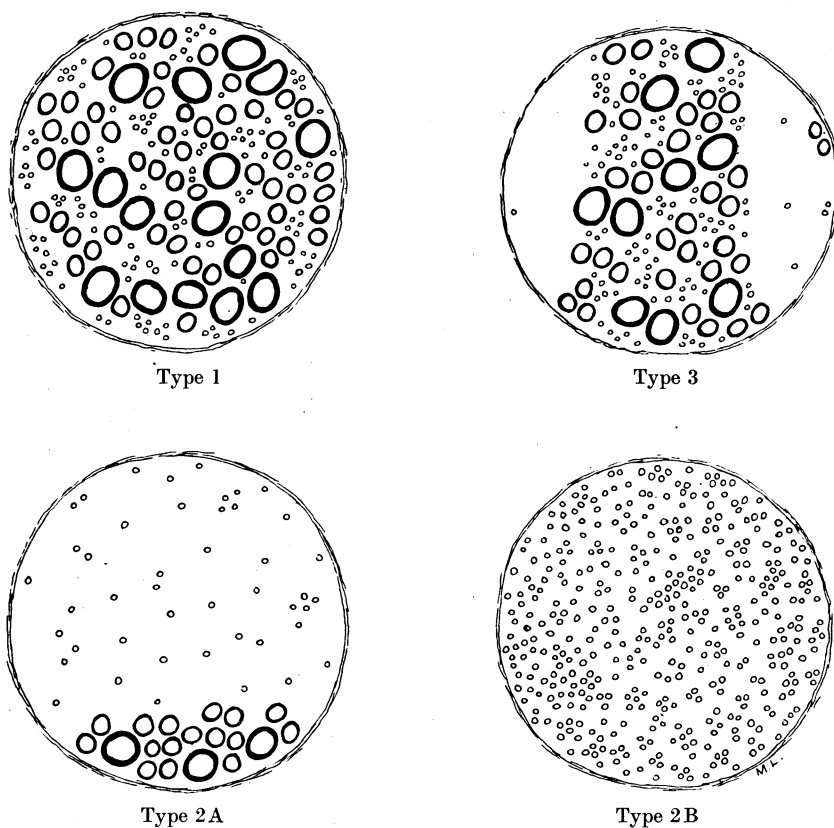


Fig. 2. Four types of rami communicantes in the rhesus monkey. Type 1 represents the white ramus; types 2A and 2B variants of the grey ramus; type 3 the mixed ramus.

within the nerve bundle a small group of ten to twenty large and medium myelinated fibres (10 to 5μ in diameter). Type 2A has been regarded here as a characteristic grey ramus. As a type it merged imperceptibly into the next.

Type 2B was heavily 'peppered' throughout with small medullated fibres under 3μ in diameter. The total number of such fibres per ramus amounted to several hundred. As in Type 2A, and again in the cervical rami, there was sometimes a small group of ten to twenty large and medium myelinated fibres (10 to 5μ in diameter). There was no sharp distinction between the two types (2A and 2B) and they have been considered here as representing different varieties of grey rami.

Type 3 was clearly a mixed ramus, one part containing myelinated fibres of all sizes and having the typical appearance of type 1, and the rest resembling the grey ramus of type 2A. The two parts were together in the same nerve bundle, and did not represent two rami running in apposition.

Types 1 and 3 proved to be restricted to the thoraco-lumbar region which, in the twenty sides recorded here, was limited by the following boundaries:

Upper level: T1	...	In 8 instances
	T2	... In 12 instances
Lower level: L3	...	In 16 instances
	L4	... In 4 instances

This corresponds closely to the outflow of small medullated fibres in ventral spinal roots. The mixed rami (type 3) occurred chiefly in the upper thoracic region, where a single ramus was the rule. The grey rami were present everywhere, but type 2B was found characteristically in the rami of C8 and T1 and of L6 and L7, which often contained several hundreds of small myelinated fibres under 3μ in diameter.

The upper cervical rami connecting the superior cervical ganglion with C1, C2 and C3 spinal nerves all belonged to type 2A. In the lower cervical region type 2B predominated. Occasionally there was a ramus composed principally of large and medium sized myelinated fibres (10 to 5μ in diameter) with a small adjacent bundle characteristic of type 2A. Since the small myelinated fibres (3μ and less in diameter) are missing, it could not be interpreted as a white ramus. The large myelinated fibres of this ramus are apparently somatic nerves to the prevertebral muscles running alongside a normal grey ramus. Wrete's embryological studies (1934-5) show this arrangement and we have confirmed it by dissection.

The first thoracic nerve was joined by a proximal and a distal ramus, and occasionally by a third, intermediate ramus. Contrary to the arrangement represented in standard diagrams, the distal and not the proximal branch was found to be the white ramus (type 1), and the others were grey (*a* in Fig. 3). This fact needs emphasizing for, although the arrangement is clearly stated by Langley (1896), Müller (1909), and Kuntz (1934), it has been largely overlooked in experimental and surgical literature.

In like manner, where the second thoracic nerve was connected by two rami, the distal of the two proved to be the white ramus. Where only one ramus joined T2 it was generally of the mixed (type 3) variety, and this was the arrangement in the succeeding five thoracic nerves (T3-T7) where each was joined usually by only one ramus. A typical nerve of the lower thoracic region (T8-T12), on the other hand, received two rami, one belonging to type 1, and the other to type 2A. A nerve of the upper lumbar region (L1-L4) was characteristically joined by two or more rami from different levels of the sympathetic cord. The upper *transverse* connexions were invariably the grey rami (type 2A) and the lower *oblique* connexions of types 1 or 3, as Botár (1932) has already shown. The rami of the lower lumbar nerves usually belonged to type 2B and were rich in small medullated fibres. In the sacral and coccygeal regions type 2A predominated, and the number of large and medium medullated fibres was negligible.

DISCUSSION

If the interpretation offered here of the four types of rami be correct, the definition of the thoraco-lumbar outflow in the monkey is essentially the same as that obtained from examination of the ventral spinal roots. It was not possible to study the constitution of the rami in the same series of animals that had been used for the ventral root investigation, but in the few examples in which both rami and spinal roots were examined the findings agreed exactly. At the upper boundary no white ramus was seen above T1 spinal nerve, and at the lower boundary none below L4. The lowest white ramus, however, ran from the third or fourth lumbar spinal nerve to join the sympathetic chain at, or below, the fifth lumbar ganglion. It would be necessary, then,

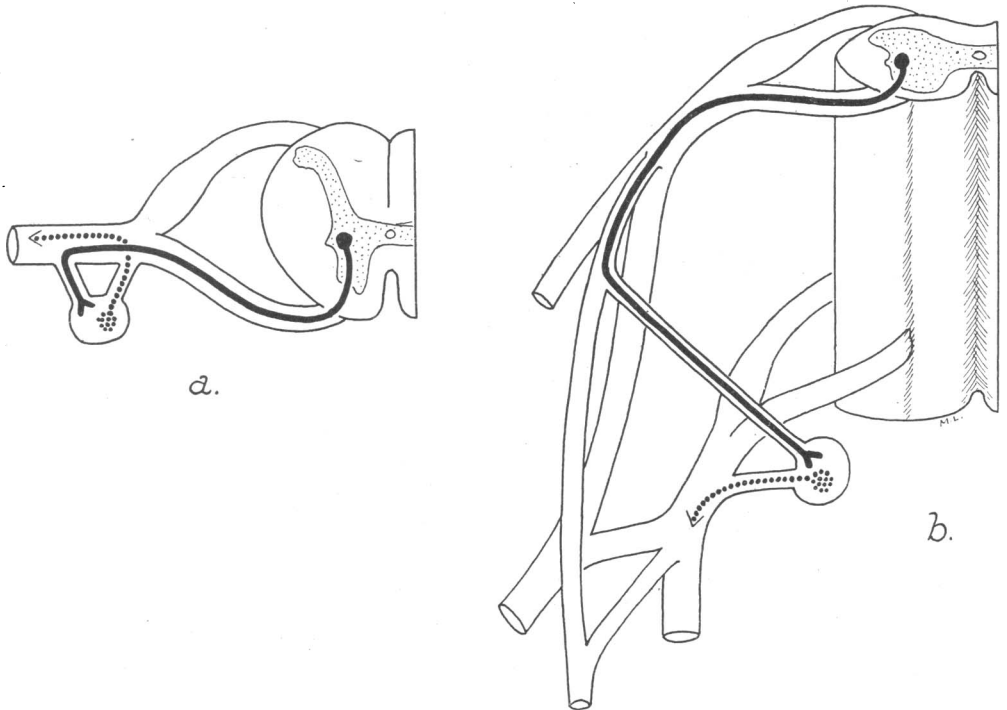


Fig. 3. Diagram of the course of the preganglionic fibre from (a) the first thoracic, and (b) an upper lumbar spinal nerve.

to divide the chain below this ganglion in order to cut all preganglionic fibres to the lower limb. Zuckerman (1938) mentions a single example where the lowest white ramus in the monkey passed out with L5 spinal nerve. It seems likely that some of the reports of an upward extension of the thoraco-lumbar outflow to C8, and even higher, are based on a misinterpretation of those rami found occasionally in the lower cervical region, composed chiefly of large and medium sized myelinated fibres and which we consider to be branches of somatic nerves to the prevertebral muscles.

The present investigation offers no support to the contention of Kiss & Mihálik (1929) that the rami cannot be differentiated histologically. It is true that the definition of what constitutes a white ramus may vary, but there can be no difficulty in dis-

tinguishing between types 1 and 3 on the one hand and types 2A and 2B on the other. There is a sufficiently sharp line of demarcation between the two groups to justify Gaskell's original subdivision into 'white' and 'grey' rami.

The white rami (type 1) are filled with medullated fibres of all sizes and, according to Ranson & Billingsley (1918), with unmyelinated fibres. Probably the larger proportion of the small medullated fibres ($3\ \mu$ and less) are preganglionic, for they undergo degeneration when the ventral spinal nerve roots are cut and degenerated. The rest of the small medullated fibres, together with the medium and large medullated, and possibly also the unmyelinated fibres, are apparently afferent in nature, for they degenerate only when the dorsal roots are divided distal to the spinal ganglia and time allowed for degeneration (Ranson & Billingsley, 1918; Kuntz & Farnsworth, 1931).

The great number of medium and large medullated fibres in the white rami is very striking, particularly in the lower thoracic region, where there occurs the greater influx of afferent fibres from the splanchnic area. Indeed, the medium and large sized fibres together far overshadow the small medullated components, so that the rami seem to define a thoraco-lumbar inflow as much as an outflow.

The presence of myelinated fibres in grey rami has long been recognized (Langley, 1896), but their occurrence in such great numbers has been underestimated. We are not here referring to the groups of ten to twenty large and medium sized fibres which may occur in grey rami, for these disappear for the most part when the dorsal roots are cut and degenerated distal to the spinal ganglia (Kuntz & Farnsworth, 1931), and are therefore generally considered to be afferent. What interpretation, however, is to be placed on the small medullated fibres which are scattered throughout a grey ramus, often, as in type 2B, in great numbers? Many persist after section and degeneration of both spinal roots distal to the spinal ganglion (Langley, 1896; Nevin, 1930; Kuntz & Farnsworth, 1931) and are therefore presumably medullated postganglionic fibres. We have been able to confirm this in the monkey (unpublished experimental data), but it is not yet clear how many fibres do degenerate following such a procedure. They are considerable in number. Langley (1896) and Wrete (1935) have suggested that some of these small myelinated fibres in grey rami may be preganglionic fibres passing to ganglion cells more peripherally placed, along the course of the grey rami ('intermediary' ganglia) or even within the spinal nerves. Examples of such intermediary ganglia, clearly recognizable grossly, have been reported here, but it seems that they may be much commoner than has been generally supposed, particularly when a microscopical search is made for them. Langley (1896) called attention to their existence, and subsequent reports have been made by Romankevich (1930) and Gruss (1932). Kuntz (1934) explains their presence as due to cells which either failed to reach the primordia of the ganglia of the sympathetic trunk during embryological development or became displaced from them. Wrete (1935) has described their frequency and distribution, and finds them located mainly in two general regions, cervical and lumbar. It is significant that the grey rami of these regions are particularly rich in small medullated fibres.

Attention has been drawn to the interconnexions between the sympathetic chains of each side, as they offer pathways through which an organ may be innervated contralaterally. The possibility of a bilateral innervation to the limbs has been weighed in attempts to explain the fact that unilateral thoracic or lumbar sympathectomy produces, in addition to its effect on the ipsilateral limb, a vasomotor change in the

corresponding contralateral limb (Simmons & Sheehan, 1939). In the monkey, however, no transverse connexions existed above the fourth lumbar level. Furthermore, no action potentials could be picked up in the sciatic nerve following stimulation of the ventral roots of the lower thoracic and upper lumbar segments on the contralateral side (Sheehan & Marazzi, 1941). The transverse connexions do not therefore appear to be concerned significantly in the innervation of the limbs.

The difference in the gross anatomy of the ganglia at various levels is most conspicuous. In the upper thoracic, lower lumbar and sacral regions the spinal nerve is almost invariably connected to the ganglion of the same segment by one or several rami. This simple segmental arrangement does not exist in the cervical or in the lower thoracic and upper lumbar levels, where a ganglion sends rami to two or more spinal nerves. In addition, it is in these regions that irregularities of the ganglia in the form of fusion, duplication or absence are most frequent. The primordia of the ganglia of the lower thoracic and upper lumbar levels presumably divide, the caudal portion of each fusing with the upper part of the next succeeding primordial mass. A permanent ganglion in these areas is then the result of fusion of portions of two succeeding ganglia, and their rami obviously join two or several spinal nerves (Fig. 4). Splitting and secondary fusion may explain the frequent anomalies of the ganglia within this region.

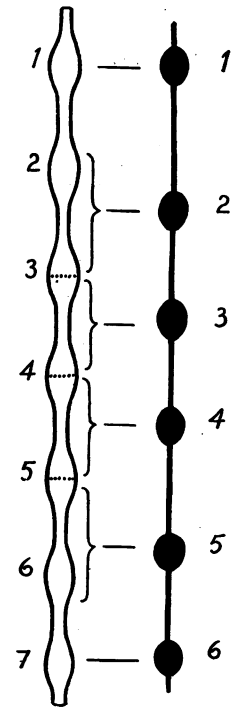


Fig. 4. Schematic representation of the development of the ganglionic chain from the primordial cell column in the lower thoracic and upper lumbar regions.

SUMMARY

1. A study of the connexions and constitution of rami communicantes in the macaque reveals four general types. One (type 1) is filled with myelinated fibres of all sizes and has been interpreted as the white ramus. Two other types (types 2A and 2B) are composed of unmyelinated fibres with differing amounts of myelinated fibres, distributed throughout the ramus. They represent variations of the grey ramus. The fourth type (type 3) is mixed, with areas of 'grey' and 'white' in the same nerve bundle.

2. The white and mixed rami do not extend beyond the limits of the thoracolumbar outflow as outlined in the previous study of the ventral spinal roots—namely T1/T2–L3/L4, rarely L5.

3. In the lower cervical region a branch of the spinal nerve to the prevertebral muscles may run with a grey ramus for the greater part of its course, and may be mistaken for a white ramus to a lower cervical nerve.

4. The small myelinated fibres (3μ or less) in grey rami may number several hundred, particularly in those of C8 and T1 and of L6 and L7 spinal nerves. Many of these fibres are myelinated postganglionic, but some may be preganglionic, reaching intermediary ganglia placed along the course of the ramus or within the spinal nerve.

5. The distal, and not the proximal, ramus to the first thoracic nerve is invariably the white ramus.

6. In the upper thoracic, lower lumbar, and sacral regions a ganglion is connected with its corresponding spinal nerve, usually by only one ramus, which in the upper thoracic region is of the mixed type. In the lower thoracic and upper lumbar regions the ganglia are larger and more irregular, and each is connected with two or more spinal nerves, by a transverse (grey) ramus with its corresponding spinal nerve, and an oblique (white) ramus descending from the spinal nerve one or two segments higher.

7. Some form of transverse connexion between the sympathetic chains of each side was found in every dissection, but never above the level of the fourth lumbar vertebra. A double sympathetic chain occurred only in the lumbar region and never extended for more than the distance between two adjacent ganglia.

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