OBSERVATIONS ON THE MEDULLATED FIBRES OF THE SYMPATHETIC SYSTEM AND CHIEFLY ON THOSE OF THE GREY RAMI COMMUNICANTES.

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SOME account of the medullated fibres of the grey rami of the sympathetic ganglia I have already given[1]. I came to the conclusion that the great majority of the small medullated fibres in the grey rami arise from the nerve cells of the sympathetic ganglia—and that a few, chiefly large fibres, arise from the cells of the spinal ganglia.

I propose to deal here more fully with the origin of these medullated nerves. It may, perhaps, seem to be a matter of little importance, except as regards the main question of whether sympathetic nerve cells do or do not give off medullated fibres. But, in fact, the number of medullated fibres in the grey rami has been greatly underestimated. Thus the grey ramus given off by the 7th lumbar ganglion in the cat may contain more than 300 medullated fibres. It is, then, essential to a proper understanding of the relation of the central nervous system to the sympathetic to know what connection, if any, these fibres have with the spinal cord.

There are very few observations which bear directly on the question. The view that sympathetic nerve cells give off medullated fibres is of very old standing. Bidder and Volkmann[2] believed that nearly all, if not all, small medullated fibres arose from either sympathetic or spinal ganglion cells. They may be regarded as having proved that in the frog, small medullated fibres are given off by the sympathetic ganglia, and that in the mammal such fibres are given off by some of the ganglia on the course of the cranial nerves. Bidder and Volkmann, it must be remembered, rejected the view that Remak's fibres were of nervous nature.

In more recent times the prevalent view has been that sympathetic

[1] *Phil. Trans.* 1892. B. p. 114; *Proc. Physiol. Soc.* XII. 1893 (This *Journal*, XV.). "A Short Account of the Sympathetic System." Separate Paper (Berne Congress), 1895.

[2] *Die Selbständigkeit des sympathischen Nervensystems.* Leipzig, 1842.

nerve cells in mammals give off non-medullated fibres only. Kölliker[1] however, in an address on the sympathetic system states that he has arrived at the conclusion that in many cases the axis cylinder process of a sympathetic nerve cell becomes medullated. And Dogiel[2], though he did not actually find any medullated axis cylinder processes in mammalian sympathetic cells, holds the same view.

We will first consider what are the possible origins of the medullated fibres of the grey rami.

1. They may arise from nerve cells in the spinal cord. In this case we should consider them to be efferent nerve fibres, although perhaps it is not quite definitely proved that every axis cylinder process sent off by a nerve cell in the spinal cord to the periphery is efferent.

They may then pass to the sympathetic, (*a*) in the grey ramus of the spinal nerve by which they leave the cord, or (*b*) in some other ramus, white or grey.

2. They may arise from cells in the spinal ganglia. In this case we should consider them to be afferent nerve fibres. But we should do so on general grounds, for if there were in the spinal ganglia cells of the sympathetic type sending off efferent medullated fibres, they would not be distinguishable by the degeneration method from afferent posterior root fibres.

The afferent fibres, as the efferent, may pass to the sympathetic, (*a*) in the grey ramus of the nerve to which they belong, or (*b*) in some other ramus, white or grey.

3. They may arise from cells in the sympathetic ganglia. Here also there are two possibilities to consider, viz. whether these fibres arise (*a*) from cells in the ganglion from which the grey ramus arises, or (*b*) from cells in some other ganglion.

Most of these possibilities can be tested decisively by the Wallerian method, and by it alone.

Before proceeding to the results of the degeneration experiments, it is necessary to state briefly the normal distribution of medullated fibres in the trunk of the sympathetic.

In the cat—with which we are chiefly concerned—the whole length of the sympathetic chain, except in the ganglia, consists in much the greater part of medullated nerve fibres. This is clearly seen both in transverse sections and in teased preparations, and in the sacral and coccygeal regions, as well as in the lumbar and thoracic regions.

[1] Kölliker. *Wiener klin. Wochensch.* Nos. 40 and 41. 1894.

[2] A. S. Dogiel. *Archiv f. mik. Anat.* XLVI. p. 305. 1895.

A certain number of non-medullated fibres are however found. At any one place, most of these form a small bundle, which can be traced from a ganglion to a neighbouring white or grey ramus[1]. In the lumbar and sacral regions when the ganglia are regularly arranged, such grey bundles, if present, run for the most part downwards, and issue at the level of the next lower ganglion. When a white ramus enters the sympathetic a short distance above a ganglion, then a grey bundle runs upwards to issue in the white ramus. When the ganglia are irregular in position—and this is frequent in the sacral region—the grey bundle may run up or down, and for a rather longer course. Thus it may happen that the Ist sacral ganglion is large, and that the IInd sacral ganglion is barely represented. In such case, grey fibres may pass in the sympathetic trunk from the Ist sacral ganglion, and from the chief part of the IInd sacral grey ramus, and even a part of the IIIrd sacral grey ramus. This I take to mean that the apparent Ist sacral ganglion is, in such case, really a compound ganglion, containing most of the nerve cells of the normal IInd sacral ganglion; just as the ganglion stellatum contains the cells of the lower cervical and of the first two or three thoracic ganglia.

A considerable portion, then, of the grey fibres of the sympathetic trunk are grey rami running with the trunk for not more than one segment.

Other non-medullated fibres, which I cannot trace into the grey rami, I think are probably the protoplasmic processes of the nerve cells ending free between the fibres and cells of the sympathetic chain.

But, as I have said, the non-medullated fibres are in a small minority in the trunk of the sympathetic in the cat.

In the rabbit the state of things is different. Here are more non-medullated and fewer medullated fibres, especially in the sacral and coccygeal regions. In the latter indeed very few medullated fibres occur. This I hold[2] is due to the pre-ganglionic fibres losing their medulla at some little distance before they make connection with the nerve cells.

In the cat, the medullated fibres of the sympathetic appear to be somewhat smaller than in the dog. In the dog, I found that most of the nerve fibres could be classed as belonging to one of three types, viz.

[1] For physiological observations on this point, cp. This *Journal*, xv. 201. 1893.

[2] Cp. *Phil. Trans.* 1892, p. 119. I there stated that medullated fibres are few below the IInd sacral ganglion. Later I found that was not the case in the cat (*Proc. Phys. Soc.* 1893), and in subsequent observations on the rabbit I have found considerably more medullated fibres in the lower sacral region than I observed then.

large fibres about 8 μ in diameter, medium fibres about 5 μ in diameter, and small fibres about 3 μ in diameter, though all sizes from 2 to 12 μ were present.

In the cat the corresponding fibres are about 7 μ, 4·5 μ and 2·5 μ; fibres from 2 to 10 μ, and occasionally of greater diameter than 10 μ, being also present. The fibres which run to the Pacinian bodies are usually 7 to 7·5 μ, but rather smaller and rather larger fibres also run to these bodies.

The large and medium fibres are most numerous in the lower dorsal and upper lumbar region. Here, too, they are somewhat larger than in the lower lumbar region. Most of them pass out in the splanchnic and inferior mesenteric branches. Below the last of these branches, and occasionally a short distance above, there are few fibres larger than 5 μ diameter. Thus between the VIIth lumbar and the Ist sacral ganglion, two to five fibres of 5 μ to 6·5 μ are usually present. There are a variable number of 3·75 to 5 μ, with deeply stained medulla. And it is by no means easy to decide whether those near the lower limit of size belong to the medium or to the small fibre class. Below the Ist sacral ganglion, the medium and large fibres diminish in number, but sometimes one and sometimes two, undoubtedly not belonging to the small fibre class, may occur at the level of the Ist coccygeal ganglion.

In the grey rami the size of the medium and large fibres varies fairly closely with the size of those in the adjoining sympathetic trunk. In the sacral grey rami fibres above 5 μ in diameter are rare, but there may be a fair number of about 4μ diameter, which differ markedly from the fibres of 2·5 μ diameter.

The term 'grey ramus' is one rather of convenience than of anatomical accuracy. In most cases, a sympathetic ganglion sends off two filaments to the corresponding spinal nerve. These often surround the vertebral artery, interlace,—at this spot there may be a group of nerve cells—and pass on as one or two obvious strands to the spinal nerve, and one or more small strands to other structures. Moreover the ganglion often sends direct one or two small filaments to the vertebral artery, aorta, or some structure other than the spinal nerve. Now and then one of these small filaments has a relatively large proportion of medullated fibres above 4μ in diameter. Occasionally when a grey ramus branches, a medium sized medullated fibre of one branch may be seen curving round into the other, without having any connection with the sympathetic ganglia.

In this account, when I speak of a grey ramus, I mean, unless

otherwise is stated, the one or two strands which run to the spinal nerve; these strands were taken near the ganglion unless this portion contained nerve cells, in which case the ramus was taken peripherally of the nerve cells. The number of medullated fibres in the portion of the grey ramus taken does not always give accurately either the number of medullated fibres which actually join the spinal nerve, or the number which issue from the ganglion. The number is however more than sufficiently accurate for my purpose. Greater accuracy is of doubtful value, since the number of medullated fibres in the grey rami varies with the arrangement of the spinal nerves, *i.e.* whether they are anterior, median, or posterior, and this is especially the case with the upper sacral grey rami.

It may be remarked that the number of small medullated fibres is in general proportional to the size of the grey ramus, *i.e.* to the number of non-medullated fibres.

Counting the number of medullated fibres is not unattended with difficulty, for many of the small medullated fibres and some 3 to 4 μ in diameter take a very faint stain with osmic acid. The strands must be teased out into very slender filaments, and examined under a bright light, with a high power; a diaphragm with large but not too large aperture should be used.

The nerves should be placed successively in 1 p. c. osmic acid for several hours to a day, in running water for half-a-day, in 75 p. c. alcohol for half-a-day, and finally in glycerine. They should be examined without long delay. If the nerves are kept in alcohol, they become brittle, the non-medullated fibres become dark, and the whole useless.

In a properly treated specimen, fibres of more than 4 μ are always deep black and very conspicuous. Fibres of less diameter, even those of 2 μ may be obvious, though naturally less conspicuous. When counting the number of medullated fibres in a specimen, I have usually counted the number of large, medium, and small fibres present. In doing so, I have reckoned fibres of about 4 μ as medium sized fibres provided they are deep-black.

In the Protocols of the experiments I have put the number of large, medium, and small fibres in order; thus in the Table on p. 61, the VIth lumbar grey ramus contained 1 large, 1 medium, and 183 small fibres which were sound, and 8 small fibres which were degenerated. This is indicated by the figures 1.1.183; 0.0.8. When only two numbers are given, the first indicates the number of large and medium fibres together.

I do not however wish to lay any great stress on the numbers of medium and large fibres noted, partly because, as I have said, fibres intermediate between small and medium, and medium and large, occur, so that slight swelling or shrinking may place the intermediate fibres in one animal in one class, and in another animal in another class, and partly because I have not in all cases actually measured the fibres.

Most of the operations mentioned in this Paper were performed in conjunction with Mr Anderson to determine either the nature of the reflex effects obtainable in the sympathetic system[1], or the distribution of the fibres of the nervus erigens[2]. All the observations were made on cats, with the exception of Exp. 9, which was made on a rabbit.

Question of Trophic Centre in the Spinal Cord.

To decide this, the nerve roots are cut, and in about a week, the sympathetic trunk and grey rami are examined. The fibres which are found degenerated may be taken to be fibres which arise from nerve cells in the spinal cord.

Exp. 1. *IInd and IIIrd Sacral and all Coccygeal Roots cut on both sides.* 12 *days.*

	Grey Rami		Trunk above Ganglion	
	Sound	Degenerated	Sound	Degenerated
II S. right	2.6.42	0	—	—
left	about 60	0	—	—
III S. right	about 30	0.1.0	very many	0
left	about 30	0		
I C.	—	—	many	0
II C. right	fair number	0.0.1	—	—
III C.	—	—	many	0.?1.1

The grey rami of the IInd and IIIrd sacral nerves contained a considerable number of fibres of 3·5 μ to 4 μ in diameter. The spinal nerves were of posterior (*a*) class.

In the experiment just given, all the efferent fibres of the 2nd sacral and lower nerves were degenerated. The grey rami of the IInd sacral ganglia contained together more than 100 medullated fibres, and not one was degenerated. The grey rami of the IIIrd sacral ganglia contained together more than 50 medullated fibres and one degenerated. One

[1] This *Journal*, XVI. 410. 1894. [2] *Ibid.* XIX. 372. 1896.

degenerated fibre was also present in the left IInd coccygeal grey ramus.

Similar results were obtained in experiments 10 to 12 (cp. pp. 65, 66). In these however some nerves were cut centrally, and others peripherally of the spinal ganglia. Selecting those in which the section was central of the spinal ganglia we have

Number of degenerated fibres in Grey Rami.

	VI L.	VII L.	I C.	II C.
Exp. 11	0	—	—	—
Exp. 12	0	1	—	—
Exp. 10	—	—	1	0

Hence then the medullated fibres of the lower lumbar and sacral grey rami do not arise from the lower lumbar or sacral spinal cord.

It is conceivable however that they might arise from higher regions of the spinal cord, especially from the nerves sending white rami to the sympathetic. This possibility was tested in the following experiments.

EXP. 2. *Ist to Vth Lumbar Roots cut on both sides.* 10 *days.*

	Grey Rami		White Rami
	Sound	Degen.	
XIII Th.	25	0	XIII Th. Many medium to large. It contains a slender grey strand with one large fibre.
IV L.	—	1	No degenerated fibres.
V L.	—	0	IV L. Great majority degen.
VI L. to V	—	0	V L. Great majority degen.
to VI	1.1.183	0.0.8	Sympathetic Trunk.
VII L.	3.7. many	0	Above XIII Th. Many large and medium. Small grey strand. No degen.
I S. left	2.5. many	0	,, VI L. Majority degen. The sound fibres are nearly all small, a few are about 4 μ.
right	many	0	,, VII L. Great majority degen.
			,, II C. Considerable number degen. Few sound small.

In a bundle of large fibres (7 to 8 μ) running to Pacinian bodies near the inferior mesenteric artery, one and perhaps two were degenerated. Three fibres entering Pacinian bodies were degenerated.

In the genito-crural nerve—consisting of large, medium, small and non-medullated fibres—6 medium to large were degenerated.

The nerve strands were examined on the left side.

EXP. 3. *Ist to VIth Lumbar Roots cut on both sides.* 13 *days.*

	Grey Rami		White Rami
	Sound	Degen.	
XIII Th.	Few	0	Two rami *to* ganglion. (1) Many medium and large fibres, very little grey; (2) few medium and large fibres, more grey. Neither any degen.
II L.	Fair number, all sizes	0	Great majority degen. Two of 12 to 13μ amongst them.
III L.	—	—	Great majority degen. including two medium to large. Sound small grey strand.
IV L.	Fair number, med. & small	1	Great majority degen. including two large, and a few medium. Sound fibres are chiefly medium.

No degenerated fibres were found in the sympathetic trunk just above the XIIIth thoracic ganglion.

EXP. 4. *XIIth Thoracic to Vth Lumbar Cord removed.* 6 *days.*

	Grey Rami		White Rami	
	Sound	Degen.		
IV L.	—	Group of 4	XI Th.	? Two or three degen.
VII L.	130	1	XII Th.	Great majority degen., including one or two large.
I S.	Some medium, many small	0	IV L.	Majority degen., including several medium.

Bundles of degenerated fibres were present in the left splanchnic nerve, but the majority were normal.

The fibres were nearly all degenerated between the VIIth lumbar and IST sacral ganglia.

At the IInd coccygeal ganglia there were many degenerated fibres, but an appreciable number were sound.

The grey rami of the upper lumbar nerves contained sound fibres much as usual; but they were not teased out, so that some degenerated fibres may also have been present.

In the following three experiments the time allowed for degeneration, viz. 17, 27 and 48 days, is sufficient for the complete absorption of the medulla of a greater or less number of degenerating fibres. They are, in consequence, chiefly available for information as to the presence of sound medullated fibres.

The experiments were made by Prof. Sherrington, in connection with

his work on sensory nerves in muscle, and he was kind enough to allow me to take the lumbar and sacral sympathetic.

Exp. 5. *Ist to Vth Lumbar roots on one side cut.* 17 *days.* The IVth lumbar grey ramus contained a moderate number of sound fibres and no degenerating. The VIth lumbar grey ramus contained many sound fibres and no degenerating.

Exp. 6. *Ist to Vth Lumbar roots on one side cut.* 27 *days.* No degenerating fibres were seen in the XIIIth thoracic grey ramus, nor in the sympathetic trunk a little below the IInd lumbar ganglion, nor in the VIth lumbar grey ramus. The latter contained a considerable number of sound medullated fibres.

Exp. 7. *IIIrd to VIth Lumbar roots on one side cut.* 48 *days.* The Ist sacral grey ramus contained some sound medullated fibres of about 5μ diameter, and a considerable number of small ones.

In Exps. 2, 3 and 4, the roots of the first five lumbar nerves were cut, there was in consequence degeneration of all the efferent fibres running to the sympathetic chain by way of the lumbar white rami. In the grey rami the number of degenerated fibres was as follows:

	II L.	IV L.	V L.	VI L.	VII L.	I S.
Exp. 2	—	1	0	8	0	0
Exp. 3	0	1	—	—	—	—
Exp. 4	—	4	—	—	1	0

All these grey rami contained about their normal number of sound medullated fibres. These sound fibres then clearly could not be efferent spinal cord fibres joining the sympathetic trunk by way of the lumbar white rami. Nor could they be efferent fibres running to the sympathetic trunk by way of the upper lumbar grey rami. And we have seen that efferent fibres do not join the sympathetic trunk by the lower lumbar or sacral grey rami.

Hence, then, the medullated fibres of the grey rami, with the possible occasional exception of a few—are not efferent fibres having their trophic centre in the spinal cord.

We may turn now to the few fibres which were found degenerated in some of the grey rami after section of the lumbar spinal nerve roots. These might be

(*a*) Degenerated fibres occurring irrespective of the operation. In peripheral nerves the occasional occurrence of degenerating fibres under apparently normal conditions has been described by several observers and especially by S. Mayer. But as I have never seen in cats, dogs and rabbits a single degenerated fibre in the sympathetic apart from some

lesion, I do not adopt this explanation of the degeneration in the grey rami.

(*b*) They might be afferent fibres injured during the operation or by pathological processes afterwards. In Exp. 2 it is clear that afferent fibres were to a slight extent implicated, for in a bundle of 11 fibres running to Pacinian bodies one fibre was found degenerated. I think it possible that this might account for one or two of the degenerated fibres of the grey rami.

(*c*) They might be efferent fibres on their way to aberrant ganglion cells. On the course of the grey rami, small groups of nerve cells are sometimes found. These nerve cells belong, I hold, to the adjoining sympathetic ganglion. Just as medullated fibres run from the spinal cord by the white rami to branch out over the cells of a sympathetic ganglion, so if a portion of a ganglion becomes separated from the rest, some spinal fibres will continue on their course until they come in touch with the cells of the separated portion. A larger number of such fibres would I think be seen, were it not that some of the medullated spinal fibres lose their medulla an appreciable distance before connecting with the sympathetic nerve cells. On this view it would be probable that the degenerated nerve fibres would disappear from the grey ramus somewhere on its course to the spinal nerve. And in fact in Exp. 2, the VIth lumbar grey ramus, which contained 8 degenerated fibres near the sympathetic ganglion, contained no degenerated fibres at its point of junction with the VIth lumbar nerve.

With regard then to the few fibres which degenerate in the grey rami after section of the upper lumbar nerve roots, we may conclude—(*a*) that they are chiefly at any rate efferent fibres joining the sympathetic by the white rami and running to aberrant sympathetic nerve cells on the course of the grey rami, and not entering the spinal nerves; (*b*) that one or two may be afferent fibres implicated by the operation.

But the most important fact to bear in mind is, that section of the roots of the first five lumbar nerves caused no degeneration at all in five out of the ten grey rami examined.

Question of Trophic Centre in the Lower Lumbar and Sacral Spinal Ganglia.

Here the nerves were cut in the vertebral canal, peripherally of the posterior root ganglia. In several of the experiments this was

not done with all the nerves, but some of them were cut centrally of the spinal ganglia.

EXP. 8. *Section Ist to IVth Sacral Nerves on Left side.* 11 *days.*

		Grey Rami		Sympathetic Trunk		
		Sound	Degen.		Sound	Degen.
I S.	Main ramus	0.0.191	0	Above II S.	Very many	1
	Two rami to artery	0.2.20	1	Above I C.	Very many, all small	0
II S.		Fair number, small	0			
III S.		1 small to medium 11 small	0			

The right VII L. grey ramus contained 1 medium to large, many small. None degenerated.

EXP. 9. *Rabbit. Ist, IInd, IIIrd, IVth, Sacral Nerves cut on Left side.* 7 *days.*

	Grey Rami		Trunk above Ganglion	
	Sound	Degen.	Sound	Degen.
I S. left	Few	4	1. many	1
right	6	1	0. 2. many	0
II S. left	0	1	0. many	2
right	—	—	0. fair number	0
III S. left	0	0		

EXP. 10. *IInd and IIIrd Sacral Nerves and Coccygeal Nerve Roots cut*[1]. 7 *days.*

	Grey Rami		Trunk above Ganglion	
	Sound	Degen.	Sound	Degen.
I S.	2. many	0	—	—
II S.	about 60	0	Many[2]	0
III S.	—	0	—	—
I C.	—	1	—	—
II C.	—	0	Few small to med. Many small	0
III C.	—	—	Many	0

[1] These nerves were cut on the left side, on which the sympathetic was examined. On the right side, the IInd sacral nerve, and the nerve roots below were cut.

[2] There were scarcely any non-medullated fibres.

EXP. 11. *VIth Lumbar, VIIth Lumbar, Ist Sacral. Right side.* 13 *days.*

The VIth lumbar nerve was ligatured centrally of the ganglion; the VIIth lumbar ganglion was cut through about its middle; the Ist sacral nerve was

ligatured centrally of the ganglion, but close to it, so that a few of the cells were injured, and a few sensory fibres degenerated.

	Grey Rami		Sympathetic Trunk	
	Sound	Degen.		
VI L.	Some medium to large, many small	0	Above I S.	Many sound; few larger than 3·5μ. 4 degen., of these 2 med. to large.
VII L.	Some medium to large, many small	0.2.0	Above II S.	No degeneration seen. Below I C. are two fibres above 4·5μ.
I S.	Some med., many small	0.4.0	Above III S.	
			Above II C.	

Exp. 12. *End of Spinal Cord excised.* 9 *days.*

Ganglia of VIth and VIIth Lumbar nerves intact; ganglia of lower nerves excised.

	Grey Rami	
	Sound	Degen.
VI L. left	Fair number	0
VII L. right	Some medium Many small	7 medium
I S. left	4μ to 6μ – 8	– 2
	3μ to 4μ – 12	– 1
	2·5μ to 3μ – 22	– 1
	1·8μ to 2·5μ – 18	– 0
right	Few medium Fair number small	? 0

No degeneration found just above IST S. right.

In the preceding experiments we are dealing entirely with the lower lumbar and sacral nerves, that is with nerves which send no white rami to the sympathetic.

Putting together the cases in which the degenerated fibres in the grey rami were counted when there was degeneration of both efferent and afferent fibres of the corresponding spinal nerve, we have

	VII L.	I S.	II S.	III S.	
Exp. 8	—	1	0	0	
Exp. 9	—	4	1	0	(Rabbit)
Exp. 10	—	—	0	0	
Exp. 11	2	4	—	—	(cp. original)
Exp. 12	—	4	—	—	

The results show decisively that the great majority of the medullated fibres of a grey ramus have not their trophic centre in the posterior root ganglion of the corresponding

nerve, and they indicate that a few fibres, chiefly medium and large, have this connection.

The next step in the inquiry was no doubt to cut the upper lumbar nerves peripherally of the spinal ganglia, in order to determine whether the white rami contain afferent fibres passing peripherally in the grey rami. This step, however, I thought might be omitted, and the same end reached by cutting the lumbar sympathetic at different levels.

Question of Trophic Centre in the Upper Lumbar Spinal Ganglia and in the Sympathetic Ganglia.

It is perhaps hardly necessary to recall that in cats in which the arrangement of the lumbo-sacral nerves is posterior or median, the Vth lumbar nerve is the last to send a white ramus to the sympathetic; and that in those in which the arrangement is anterior, the IVth lumbar nerve has the last white ramus instead of the Vth. The white ramus does not run to the sympathetic ganglion corresponding to its own spinal ganglion, but to the one next below this; the lower white rami usually join the sympathetic trunk a little distance above the ganglia. And there may be two white rami from one spinal nerve.

Exp. 13. *Sympathetic cut above Vth Lumbar Ganglion, including White Ramus from IVth L. on left side. 7 days.*

		Grey Rami		
		Sound	Degen.	
IV L.	Small branch	4.4.11	0	Trunk below IVth ganglion; no degeneration.
	To IVth nerve	6.24	0	The ramus to the IVth nerve was taken peripherally of a small ganglion on its course.
V L.	Upper branch	2.2.45	0.3.15	Just above Vth ganglion, no sound fibres seen.
	Lower branch	about 30	0.2.8	The lower branch was taken peripherally of a small ganglion.
VI L.	To (?) Vth nerve	2.2.52	0.1.0	
	To VI upper br.	0.2[1].3[2].25[3]	0.1[1].4[2].6[3]	[1] About 5μ. [2] About 3μ. [3] 2·5μ or less.
	,, lower br.	0.2.4.23	0.0.0.2	
VII L.	To VIIth nerve	0.6.319	0.1.20	
	To other tissues	0.4.100	0.0.3[4].0	[4] Nearly 4μ.
I S.		1.2[4].66	0.1.6	
II S.	Main branch	1.3.21	0.1.0	From the Ist sacral downwards there were very few sound fibres in the sympathetic trunk, of these one or two were about 4μ in diameter.
	Small branch	3.6.15	0.0.1	
III S.		0.1.40	0.0.0	
I C.		0.2.77	0.0.0	
	Br. to artery	0.0.30	0.0.9	

The nerves were examined on the cut, *i.e.* on the left side.

There was a small white ramus from the vth lumbar nerve, joining the sympathetic below the vth lumbar sympathetic ganglion; most of its fibres ran obliquely to the mesentery, a part descended, and a part ascended issuing in another strand running to the mesentery. It contained 9 fibres 5μ to 10μ in diameter, and many small; none were degenerated. A grey ramus running with it contained, sound 5.5, degenerated 1.4 fibres.

EXP. 14. *Sympathetic Trunk cut between Vth and VIth Lumbar Ganglia on left side.* 8 *days.*

	Grey Rami		
	Sound	Degen.	Trunk above Ganglion
VI L.	—	—	Nearly all degen. ?6 sound. Small.
VII L.	0.1.270	0.1.6	
II S.			Nearly all degen.

EXP. 15. *Sympathetic cut on both sides between VIth and VIIth Lumbar Ganglia.* 6 *days.*

			Grey Rami	
			Sound	Degen.
VII L.	Right	To vith nerve[1]	3.13.27	0.1.12
	Left	To vith nerve	5.14.85	0.2.6
I S.[2]	Left		0.13.11	0.5.7

Just above the 1st coccygeal ganglion there were many degenerated fibres, and a few sound, of the latter 3 were medium to small.

[1] The ramus was given off from the upper end of the VIIth ganglion; it was considerably larger on the left than on the right side.

[2] The Ist sacral nerve was small, the arrangement of nerves being markedly anterior.

EXP. 16. *Sympathetic Trunk cut below VIIth Lumbar Ganglion on left side.* 6 *days.*

	Grey Rami					
	Sound	Degen.	Trunk above Ganglion			
I S.	124 abt.	1.1.5	All degen. except ?7; 1 or 2 large degen.	Right grey ramus	1.1.125	No degen.
II S.			Great majority degen., but fair number sound	Right trunk	8 to 10 degen.	

The experiments show that section of the sympathetic trunk causes distinctly greater degeneration in the grey rami than is caused by section of the roots of the lumbar nerves or of the sacral nerves

peripherally of their ganglia. Thus the number of degenerated fibres in the several grey rami, including the small branches given off by the ganglia, was

		V L.	VI L.	VII L.	I S.	II S.	III S.	I C.
Exp. 13.	Cut above V L.	28	14	21	7	2	0	0
Exp. 14.	Cut above VI L	—	—	7	—	—	—	—
Exp. 15.	Cut above VII L.	—	—	r. – 13[1] l. – 8	12	—	—	—
Exp. 16.	Cut above I S.	—	—	—	7	—	—	—

[1] To VIth nerve.

But the number of degenerated fibres—except in the case of the Vth ganglion in Exp. 13,—which may have been directly affected—is a small proportion of the total number of medullated fibres in the grey rami.

Consequently the great majority of the medullated fibres in the grey rami must arise from the cells of the sympathetic ganglia.

Moreover since the number of degenerated fibres in the grey ramus of the Ist sacral is practically the same whether the sympathetic is cut above the Vth lumbar or above the Ist sacral ganglion we may conclude, that the great majority of the medullated fibres of the grey rami arise from the nerve cells of the corresponding sympathetic ganglion.

The same conclusion is reached by a somewhat different line of argument. When the sympathetic trunk is cut below the last white ramus, nearly all the fibres in the trunk below degenerate, whilst, as we have seen, the degeneration in the grey rami is comparatively slight. If then the grey ramus is one which contains a considerable number of medullated fibres, it may be obvious that there are more medullated fibres in the ramus than in the trunk of the sympathetic above or below the ganglion from which the ramus arises. This was the case, for example, with the IIIrd sacral grey ramus in Exp. 13. The sympathetic above and below the ganglion and the grey ramus given off by it were teased out—without being separated from the ganglion. The preponderance of medullated fibres in the grey ramus was most striking. Similarly if serial longitudinal sections be made of a ganglion, such as the VIth or VIIth lumbar or the Ist sacral after section of the sympathetic above the VIth lumbar ganglion, the rarity of sound fibres above and below the ganglion and the rarity of degenerated fibres in the grey ramus are equally conspicuous

features. In such sections, when the ramus, as is normally the case in the lumbo-sacral region, is given off from the lower end of the ganglion, the medullated fibres of the ramus are seen to run upwards, spreading out fan-ways through all parts of the ganglion. Since, as I have shown above, the sacral nerves send at most an insignificant number of fibres to the grey rami, it follows that some of the nerve cells of the ganglion give off medullated nerve fibres[1].

In Exp. 16 the VIth and VIIth sympathetic ganglia were excised. In the corresponding grey rami nearly all the fibres were degenerated. Longitudinal sections were made of the VIth lumbar nerve at the spot where the grey ramus joins it. The ramus divided, the larger part running peripherally, the smaller part centrally, and close underneath the sheath of the nerve. Degenerated fibres were present in both.

Since, then, the nerve cells of the ganglia of the sympathetic trunk send off a certain number of medullated fibres, we should expect that the same would be the case with other similar ganglia. Some facts in favour of this have already been brought forward by Mr Anderson and myself. We found that a few small medullated fibres were still present after degeneration of the rami to the inferior mesenteric ganglia[2], and a few also in the nervus erigens—after section of the sacral nerves[3].

The strands given off by the superior cervical ganglion of the cat offer an easy field for the investigation of the question; these, as I have mentioned earlier[4], contain many small medullated fibres. Section of the sympathetic in the neck, *i.e.* centrally of the superior cervical ganglion, causes, as has been known since Waller's observation in 1852, degeneration of the nerve up to the ganglion. This degeneration is complete. I have not found a single sound fibre out of the 2000 or more which occur in this region. On the other hand, peripherally of the ganglion there is not a single degenerated fibre.

The medullated fibres, then, in the branches of the ganglion are either running from the ganglion cells, or else running to them from one of the cranial nerves.

On section of the branches peripherally of the ganglion, nearly all

[1] When a normal grey ramus has a small ganglion on its course, it may sometimes be seen that the number of medullated fibres is less peripherally of the ganglion, than centrally.

[2] This *Journal*, XVII. 184. 1894. [3] *Ibid.* XIX. 377. 1896.

[4] *Ibid.* XVIII. 283. 1895. In the Paper 'cut' p. 283, line 25, is a misprint for 'cat'.

the fibres which remain connected with the ganglion are unaffected, whilst nearly all the fibres separated from the ganglion degenerate.

Hence, then, nearly all the medullated fibres contained in the nerve strands given off by the superior cervical ganglion arise from nerve cells in that ganglion.

As to the remaining fibres I have shown[1] that in the dog there are usually two small bundles which pass from the tympanic plexus to the internal carotid artery, and run thence to the superior cervical ganglion by the side of the anterior branches of the ganglion. Probably in the cat there are some homologous nerve fibres.

The facts given above, allow some further conclusions to be drawn. More fibres degenerate in the grey rami when the lumbar sympathetic trunk is cut than when the anterior roots from the XIIth thoracic to the Vth lumbar are cut. We have seen reason to believe that the upper lumbar sympathetic ganglia do not send medullated fibres to the lower lumbar rami. And we may reasonably conclude that some proportion of the fibres which degenerate in the grey rami as the result of cutting the sympathetic trunk are afferent fibres having their trophic centre in the spinal ganglia of the nerves which send white rami to the sympathetic. These fibres are of all the sizes, which are proper to grey rami.

The experiments give some support to the view that a few fibres of the grey rami, chiefly medium, and large, are afferent fibres arising from the posterior root ganglion. This in Exp. 15, in the sacral region all the fibres coming from white rami were degenerated. Nevertheless the grey ramus given off by the VIIth lumbar ganglion to the VIth lumbar nerve contained fibres varying in diameter from 4μ to $6{\cdot}5\mu$. Bearing in mind the results of section of the sacral nerves peripherally of the posterior root ganglia, it is reasonable to suppose that some of these fibres arose from the posterior root ganglion of the VIth spinal nerve.

Such fibres ought when stimulated to produce reflexes of one sort or another even though slight. But in some experiments made earlier[1], I could not find with certainty reflex action of any kind on stimulating either end of the grey rami of the lower lumbar or sacral nerves. It is clearly desirable to make further experiments on this point.

We may pass now to some accessory matters arising out of the foregoing observations.

[1] *Proc. Physiol. Soc.* p. ii (This *Journ.* XIV. 1893).

1. *Decussation of medullated pre-ganglionic fibres in the sacral region.* The spinal nerves which send fibres to the sacral and coccygeal ganglia have a bilateral action on the hairs of the tail[1] and on the external generative organs and genital skin[2]. The sacral and coccygeal grey rami have a unilateral action. Hence nervous impulses passing down the lumbar sympathetic of one side have a path open to them to the rami of the sacral and coccygeal ganglia of the opposite side. Such a path might be offered by processes of sympathetic ganglion cells, *i.e.* by post-ganglionic fibres, or by decussating fibres from the white rami, *i.e.* by pre-ganglionic fibres. On section of the lumbar sympathetic on one side, the former will not be recognisably affected, but the latter will degenerate, and if they are medullated, the degeneration will be easily seen.

In Exp. 13 (see p. 67), in which the lumbar sympathetic was cut on the left side, the Ist coccygeal ganglia of both sides were examined. There were two strands connecting the ganglia. The medullated fibres in these strands were all small; 30 of them were sound, 43 were degenerated. No degeneration was found in the grey ramus to the Ist coccygeal nerve. In this case then about 40 medullated fibres passed from the lumbar nerves to the nerve cells of the opposite coccygeal ganglion.

In this, and in other cases, the trunk of the sacral sympathetic on the uncut side showed a few but only a few degenerated fibres, thus in Exp. 14 (cp. p. 68) there were only 5 degenerated fibres between the Ist and IInd sacral ganglia on the side opposite the lesion. It appears then that most pre-ganglionic fibres which decussate run direct to the opposite ganglion, and a few only continue on in the opposite sympathetic trunk. It is obvious however that irregularities in the position of the ganglia, might modify this arrangement.

Mr Anderson and myself[3] found that many medullated fibres decussated in the inferior mesenteric ganglia, and passed down the opposite hypogastric nerve. Similarly in Exp. 13, given above, there were many degenerated fibres in the hypogastric of the left side—on which the sympathetic was cut—and 75 in the hypogastric of the right side—on which the sympathetic was intact.

2. *Course of the lumbar white rami.* Both from dissection and from physiological observation I have described the lumbar white

[1] This *Journal*, xv. 179. 1893.
[2] *Ibid.* xix. 87. 1895.
[3] *Ibid.* xvii. 186. 1894.

rami as running downwards in the lumbar sympathetic, and as sending to it no ascending fibres. This is confirmed by the degeneration method. Section of the roots of the Ist lumbar nerve (Exps. 2 and 3, cp. pp. 61, 62) caused no degeneration at the XIIIth thoracic sympathetic ganglion.

In Exp. 13, the section of the sympathetic was made so that any fibres—afferent or efferent—ascending the sympathetic from the white rami of the IVth or Vth lumbar nerves would degenerate. But in the sympathetic trunk above the point of section there were no degenerated fibres.

Since the white ramus of a given lumbar nerve joins the sympathetic below the ganglion corresponding to the nerve, it is probable I think that in some cases a few fibres ascend the sympathetic trunk as far as the corresponding ganglion, so that for example a few fibres from the first lumbar white ramus, joining the sympathetic near the IInd lumbar sympathetic ganglion, might ascend the sympathetic as far as the Ist lumbar sympathetic ganglion.

And for a similar short distance, a portion of a white ramus, simply traversing the sympathetic on its way to a collateral ganglion, may run upwards in the sympathetic. Thus in Exp. 13 the Vth lumbar white ramus, which was sound, sent two branches to the inferior mesenteric ganglion; one branch ran obliquely downwards, straight through the sympathetic trunk to the mesentery; the other ascended the sympathetic for about a centimetre and then ran to the mesentery in company with a large strand of degenerated fibres from the IVth lumbar white ramus.

Another point in connection with the white rami is touched on in Exp. 4. Here the cord was cut at or about the junction of the roots of the XIth and XIIth thoracic nerves. The white ramus of the XIth nerve had at most a few degenerated fibres. It follows that few if any of the efferent fibres of the XIth white ramus have their origin from cells in the spinal cord below the XIth thoracic segment. That the anterior root fibres of the thoracic nerves arise mainly at any rate from their corresponding segments of the cord has been shown by Sherrington[1] and by Grünbaum[2].

Finally I may say that the observations on the degeneration of fibres passing from the white rami, through the sympathetic to the splanchnic nerves and to the corresponding inferior mesenteric nerves,

[1] This *Journal*, XIII. 707. 1892. [2] *Ibid.* XVI. 376. 1894.

are entirely in favour of the view that these fibres have no connection with the nerve cells of the ganglia of the sympathetic trunk.

3. *Relative number of efferent and of afferent fibres in the white rami.* It has been shown by Mr Anderson and myself that the branches of the white rami which run to the inferior mesenteric ganglion have a much larger proportion of efferent than of afferent fibres, and that in the hypogastric nerve the proportion is about 10 to 1. A similar preponderance is shown by the white rami themselves. On teasing out the white ramus of a nerve the roots of which have been cut (Exps. 3—5) it is obvious that the number of degenerated fibres is largely in excess of the number of sound ones.

4. *Degeneration in the sympathetic trunk above the point of section.* In the experiments on section of the lumbar and upper sacral sympathetic trunk there were very few, and sometimes no fibres degenerated above the point of section. The facts are given in the following table.

	Place where sympathetic cut	Result	
Exp. 13.	Above Vth Lumbar ganglion	Below IVth Ganglion	— no degen.
Exp. 14.	Above VIth ,, ,,	Below Vth ,,	— 4 small degen.
Exp. 16.	Above VIth ,, ,,	Below Vth ,,	— 4 small degen.
		Above Vth ,,	— no degen.
Exp. 15.	Above VIIth ,, ,,	Right side, below VI	— no degen.
	Both sides	Left side, above VI	— 1 degen.

The few fibres which degenerated were probably post-ganglionic medullated fibres of a small grey ramus, such as we have said (p. 57) may run upwards in the trunk for not more than a segment.

Two conclusions may be drawn from the facts.

In the first place, we may conclude that, if there are fibres of the nature of commissural fibres, connecting cells of one ganglion with cells of another, such fibres are not medullated. I have already argued that the cells of one ganglion do not send impulses to the cells of any other ganglion and to that point I shall return in a later Paper.

In the second place, we may conclude that the sympathetic ganglia do not contain cells of the nature of spinal ganglion cells, at any rate so far as concerns the fibres which pass down the sympathetic from the white rami. For if there were, section of the sympathetic trunk would cause degeneration of fibres in the trunk above, in the white rami and in the posterior roots. In Exp. 13, a white ramus was cut, the central end of this showed no degeneration. And Mr Anderson and myself[1] found earlier that section of the strands running from the sympathetic

[1] This *Journal*, XVII. p. 184. 1894.

to the inferior mesenteric ganglion—practically branches of the white rami—may cause no degeneration in the central ends.

This result would of course necessarily follow from Waller's statement that section of a spinal nerve peripherally of a posterior root ganglion causes no degeneration in the nerve roots. It has however been said by more than one observer that the statement does not hold absolutely. Mr Anderson and myself have noticed some degenerated fibres (10 to 20), nearly all large, in the posterior roots of the sacral nerves after section of the nerves in the vertebral canal peripherally of the spinal ganglia. But we are inclined to attribute this degeneration to accidental injury of the nerve roots. It may be doubted whether conclusive results will be obtained except by section of the nerves outside the vertebral canal. To effect this section, so as to include the white ramus communicans, considerably increases the difficulty of the operation. Hence, then, I have thought it worth while to give above the result of direct observations on the sympathetic ganglia.

5. *The maximum size of nerve fibre given off by the sympathetic nerve cells.* My observations are not decisive on this point, but in view of the number of fibres of about 4μ diameter which may be present in the grey rami after degeneration of the fibres descending the sympathetic, I think that some of this size must be of sympathetic origin.

With regard to the medullated fibres given off by the sympathetic nerve cells, various possibilities suggest themselves. They might be fibres having some special function, such as inhibition, or they might pass to a special tissue as the erector muscles of the hairs. Or again they might be a temporary condition of the ordinarily non-medullated sympathetic fibre. But as all of these possibilities seem to me to have weighty reasons against them, I do not think it necessary to discuss them. The analogy of the medullated fibres proceeding from the ciliary ganglion points to their being efferent visceral fibres; and it is not impossible that the reason for the existence of both is of a phylogenetic nature.

General Conclusions.

In the cat the grey rami communicantes of the ganglia of the sympathetic trunk and the rami given off by the superior cervical ganglion contain a variable but often considerable number of small

medullated fibres. Thus the grey ramus of the VIIth lumbar ganglion may contain 300.

The great majority of these fibres arise from sympathetic nerve cells in the corresponding sympathetic ganglion.

In some cases, but not always, a few arise from sympathetic cells in an adjoining ganglion.

No efferent fibres run from the spinal cord to the sympathetic, by way of the grey rami. That nearly all the efferent visceral fibres run to the sympathetic by the white rami was shown, it is well known, by Gaskell. The rule stated by him is then absolute.

In some cases, but not commonly, a few efferent medullated fibres, passing to the sympathetic by the white rami, leave the sympathetic by the grey rami. These are to be considered as fibres on their way to aberrant sympathetic nerve cells lying in the grey rami before they reach the spinal nerves.

The afferent medullated fibres of the grey rami are of various sizes, 2μ, 4μ, 6μ, and in some cases 8 to 12μ. These are few in number and rapidly diminish (especially those of more than 4μ diameter), in passing from the lower lumbar to the coccygeal rami.

Most of the afferent fibres join the sympathetic by white rami, but there is some evidence that a few, especially the larger ones, may run to the sympathetic by the grey rami.

In the Rabbit, the grey rami contain hardly any medullated fibres, and it is not clear that in this animal the sympathetic cells give off medullated fibres.

The white rami of the upper lumbar nerves contain many more efferent than afferent fibres. They consist of two parts, one part runs through the sympathetic towards the mesentery without sending any filaments to the ganglia of the sympathetic trunk; the other part descends the sympathetic trunk. Normally, no fibres from the white rami ascend the sympathetic trunk.

None of the afferent fibres of the white rami have their trophic centre in the sympathetic ganglia.

The lower white rami of one side send some medullated fibres to the sacral and coccygeal sympathetic ganglia of the opposite side.

In the lumbar and sacral regions, the nerve cells of the sympathetic ganglia do not send medullated fibres to the ganglia above them, nor in all probability do they to ganglia below them.