ON EFFERENT FIBRES IN THE POSTERIOR ROOTS OF THE FROG.

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PART I.

THE accuracy of the belief that the posterior roots of nerves consist exclusively of afferent fibres, has been challenged in recent years. Vejas[1] and Joseph[2] were the first to raise the question. They asserted that in *mammals* certain fibres, which had their centre in the anterior horn of the cord, passed out by the posterior root. Their observations, however, are not very convincing, and Sherrington[3] was unable to confirm their result by means of degeneration. The balance of evidence, in fact, is against the view that efferent fibres exist in the posterior roots of mammals. On the other hand there is distinct evidence that such fibres do exist in the *chick*. Ramón y Cajal[4] found in the chick by the modified Golgi method, that at times the axis-cylinder process of a cell in the anterior horn could be traced directly into the posterior root. This was confirmed by Kolliker. Kolliker made similar observations on mammals but with a negative result[5].

Recently Steinach[6] has taken the matter up from the experimental side. He found that stimulation of the posterior roots in the *frog* caused certain visceral movements. It appeared, then, as if, in the highest series, the afferent fibres had been kept entirely distinct and separate from the efferent, while in the lower animals this separation was not so complete. If in the chick the two sets of fibres were not

[1] *Beiträg. z. Anatomie und Physiolog. der Spinalganglien.* 1883.
[2] *Archiv für Anatomie und Phys. Physiologische Abtheilung.* 1887, p. 296.
[3] This *Journal*, XVII. p. 211. 1894.
[4] *Anat. Anzeiger.* 1890, p. 112.
[5] *Handbuch der Gewebelehre*, II. p. 76. 1893.
[6] *Pflüger's Archiv*, LX. p. 593.

quite separated from one another, we should expect to find in the frog, a member of a lower series still, a more obvious mingling of the two sets of fibres in the posterior roots. This caused Steinach's statement to appear not improbable, and I decided, therefore, at Dr Langley's suggestion to repeat his experiments. Here, also, I should like to take the opportunity of thanking Dr Langley for the kind help and advice which he has freely given me.

The innervation for the frog's viscera, as given by Steinach, is as follows:

Œsophagus	Vagus and posterior roots of 2nd and 3rd spinal nerves.
Stomach	Vagus and posterior roots of 3rd, 4th and 5th (?) spinal nerves.
Small Intestine (Upper part)	Vagus and posterior roots of 4th and 5th spinal nerves.
Small Intestine (Lower part)	Posterior roots of 5th and 6th spinal nerves.
Rectum	Posterior roots of 6th and 7th, and anterior roots of 6th and 7th spinal nerves.
Bladder	Posterior roots of 7th, 8th and 9th spinal nerves, chiefly 8th and 9th. Anterior roots of 7th, 8th and 9th spinal nerves, chiefly 8th and 9th.

On reading through the description given by Steinach of his experiments, I felt considerable doubt whether the method adopted was a trustworthy one. His process was to lay the frog flat on its abdomen, and then, after preparing the roots, to cut through the postero-lateral muscles alongside the vertebral column, reflect the flap and pull out the viscera, so as to have them exposed to view. This was a simple way of performing the experiment, but it is open to the following objection: the intestines of the frog are extremely apt, on exposure, to pass into a state of auto-peristalsis; so much so, that any derangement of them should as far as possible be avoided, especially one so serious as that brought about by Steinach's operation. It is only necessary to work a very short time at the subject to see what a frequent occurrence this auto-peristalsis is. The slightest exposure was, I found, sometimes enough to send the stomach and intestines into automatic contraction, while on rare occasions even the bladder was seen to be in a state of rhythmical contraction. This necessitated a very large number of experiments and it was not till after I had performed these, that I came to a final conclusion.

In view of this difficulty, my object was to disturb the viscera as little as possible. In performing an experiment, therefore, the brain was first pithed and the nerve roots exposed: then, instead of placing the frog in the manner recommended by Steinach, I turned it on its side and made a cut in the lateral muscles of the abdomen. By this means I was able to keep the electrodes below the level of the cord, and secondly to see the various viscera without disturbing them to any appreciable extent.

The animals used were chiefly freshly caught large English frogs, though I also made use of some large frogs which Prof. Steinach very kindly sent me from Hungary as material for my work, and for which I should like here to express my thanks.

In all I performed some 150 experiments, and the conclusion to be drawn from them is distinctly unfavourable to the view put forward by Steinach, that the posterior roots contain efferent fibres for the viscera. I have time after time got no contraction of the viscera whatever, on stimulating the posterior roots of the nerves, however strong the stimulus, though this was readily obtained with a weaker stimulus on stimulating the anterior roots. Many experiments, it is true, had to be discarded, owing to the fact that the viscera were in a state of auto-peristalsis at the time of observation; but I have records of over a hundred experiments, in which the viscera were quiescent and in all of these I got perfectly clear negative results. All the posterior roots from the 2nd to the 10th were stimulated at various times: most of the observations, however, were made on the 6th to the 10th roots, as with these long roots it was more easy to insure against spread of current than was the case with the shorter roots. The following experiment is one which I performed with a view of ascertaining whether the bladder was supplied with efferent fibres by the posterior roots: it will serve as a sample of the rest. The roots stimulated were those which, according to Steinach, caused contraction of the bladder, viz., the 7th, 8th, 9th, and 10th. The 10th was stimulated, because it was said at times to send efferent fibres to the bladder, though its action was not constant. I also examined the anterior roots of the same nerves with the following results. I started with a stimulus of medium strength and increased the strength subsequently :—

Nerve	Root	Pointer of secondary coil at	Duration of stimulus	Result
7	Posterior	20 cm.	20 sec.	No contraction of bladder
8	Posterior	20	20	,, ,,
9	Posterior	20	20	,, ,,
10	Posterior	20	20	,, ,,
7	Anterior	20	20	,, ,,
8	Anterior	20	20	,, ,,
9	Anterior	20	3	Immediate contraction of bladder
10	Anterior	20	3	Slight contraction of bladder

The secondary coil was then pushed up, till the pointer was at the 14th cm. The difference between the results now obtained and those given above, was that on stimulating the anterior root of the 7th nerve, contraction immediately resulted, and the contraction following stimulation of the 10th anterior root was more marked than previously. No contraction followed stimulation of the 8th anterior or any of the last four posterior roots.

Lastly the secondary coil was pushed up still further, to the 9th cm. The results were the same as before, contraction following immediately on stimulating the anterior roots of the 7th, 9th and 10th nerves, but not in the least degree on a stimulus applied to the 8th anterior and the 7th, 8th, 9th and 10th posterior roots.

It will thus be seen that whereas a moderately weak stimulus applied to the anterior roots of some of the spinal nerves was sufficient to cause contraction, a much stronger stimulus applied to the posterior roots was unable to effect the same. The result was really more marked than appears above, for I found that an extremely weak stimulus (the pointer of the secondary coil was 33 cm. away) when applied to the 9th anterior root was sufficient to cause contraction of the bladder, while, as has been said, a very strong stimulus to the posterior roots gave no result.

The coil used was an ordinary Du Bois coil, with one Daniell cell. The strength was such that the current was just felt on the tongue when the pointer of the secondary coil was at 19 cm., and was felt as a very strong stimulus, with the coil at 11 cm.

This experiment is only one of many, and the conclusion therefore arrived at, is that efferent fibres to the frog's viscera do not pass out through the posterior roots, and that, if care be taken firstly, to prevent spread of current, and secondly, to eliminate the very high percentage of experiments in which the viscera are in a state of peristalsis, it can be shown that stimulation of the posterior roots does not cause contraction of the bladder and intestines.

But though I am unable to confirm Steinach's assertion that the *viscera* derive some of their motor fibres from the posterior roots, I do find that in some cases efferent fibres pass out by the posterior roots to the *skeletal muscles*. Whether they exist in the posterior roots of all the nerves I do not know, as I confined my attention to the 6th, 7th, 8th and 9th nerves, more especially the last two. The animals used were in all cases Rana Temporaria. These efferent fibres to the muscles are only found in a minority of frogs examined.

Taking the 9th posterior root on both sides and stimulating it with a tetanising current, I find that in about one out of every six frogs, I get contraction of some muscle: the muscle in question differs in different frogs. I have not as yet found the posterior roots on both sides in any one frog containing these efferent fibres. It has always been confined to one side or the other.

The same may be said of the 8th posterior root, the only difference being that this root contains efferent fibres rather more often than does the 9th, the average, taking the roots on both sides, being about once out of every four frogs. In one frog I found the 8th posterior roots on both sides supplied efferent fibres to the semimembranosus, but with this exception, the efferent fibres were confined to one side or the other, just as was the case with the 9th nerve.

The 7th posterior root does not contain these fibres very often: they may perhaps be expected in 5 p.c. of the frogs examined.

The 6th nerve was only examined eleven times: in none of these, however, did I get contraction of any skeletal muscle.

The muscles in the various instances differed. I have succeeded in getting contraction of some muscle in 30 cases altogether. As will be seen from the list below, the semimembranosus is supplied by these

Posterior root	7	8	9	Total
Muscles supplied by these efferent fibres				
Semimembranosus	0	11	2	13
Flexor digitorum	0	3	3	6
Gastrocnemius	0	2	1	3
Rectus internus minor	0	1	2	3
Rectus anticus femoris	0	2	0	2
Extensor digitorum	0	0	2	2
Oblique muscles of abdomen	1	0	0	1
Total of muscles thus supplied	1	19	10	30

fibres far more often than any other muscle, and this is more especially the case with the 8th posterior root. The list shows what muscles are supplied by fibres from the posterior roots, and the number of times I have been able to get contraction of each muscle on stimulating the 7th, 8th and 9th posterior roots.

As a rule stimulation of any one root caused contraction of one muscle only, but in three instances the 8th root contained efferent fibres for two muscles (in one case the gastrocnemius and semimembranosus, and in the other two the rectus anticus femoris and semimembranosus) and it was therefore only in 16 cases that the 8th root contained these fibres.

In all 125 9th posterior roots were examined:

In all 125 9th posterior roots were examined:	efferent fibres were found in	10 cases	=	8 p.c.
„ 128 8th	„ „ „ „	16 „	=	12·5 p.c.
„ 38 7th	„ „ „ „	1 „	=	2·5 p.c.
„ 11 6th	„ „ „ „	0 „	=	0 p.c.

It is sometimes the case that in any one frog the 8th posterior root on one side and the 9th on the same or the opposite side will both contain efferent fibres, and, as a result, we meet with these fibres (taking the 7th, 8th and 9th roots on both sides) in about one frog out of every four; not more often.

In most cases the posterior roots only partially supply the muscles; the corresponding anterior roots also sending efferent fibres to the same muscles. In one instance, however, the rectus anticus femoris received its efferent fibres entirely from the posterior root of the 8th nerve.

There can, I think, be no doubt that the contraction of these skeletal muscles is really due to efferent fibres passing in the posterior roots. It is certainly not due to spread of current; for if this were the cause, it is difficult to see why, even with a very strong stimulus, any definite muscle should be picked out, and why we should get contraction in only a limited number of cases: and, further, if a posterior root be seen, on stimulation, to cause contraction of a muscle, a weak stimulus is sufficient to cause this contraction, while not the slightest contraction can be got on stimulating the majority of posterior roots, though the stimulus may be extremely strong. The stimulus required, in the few cases that give contraction, is surprisingly weak. I have in one instance got contraction of the rectus internus minor on stimulating the 8th posterior root with an electric current, when the pointer of the secondary coil was as much as 53 cm. away; and in another case contraction of the semimembranosus resulted on a stimulus to the nerve only slightly stronger, the pointer being 50 cm. off. The current is too weak to make it in the least degree likely that the contractions are caused by a spreading of the current. Moreover, placing the electrodes in a little fluid, which had collected near the ganglion of the nerve, did not cause contraction of this or any other muscle. The current was so feeble, that, to have any effect, the stimulus had to be applied to the nerve direct. Again, contraction can be got without the use of electrical stimulation at all. Mechanical stimuli, such as pinching the nerve with forceps or crimping it, are sufficient to cause a contraction.

Lastly, it was just possible, though not at all likely, that it might be in some way due to a kind of reflex action through the cord. This is not the case, however; for I took four instances in which stimulation of the 8th or 9th posterior roots gave contraction, and then cut out the whole cord. When this had been done the root was again stimulated both electrically and mechanically. In all cases the contraction was as marked as it was before.

I think, therefore, that there can be no doubt that, sometimes, efferent fibres to the skeletal muscles exist in the posterior roots of the frog's spinal nerves.

PART II.

I propose here to deal with the innervation of the frog's viscera: Waters[1] stated some time ago that strong stimulation of the 3rd, 4th, 5th and 6th nerves causes contraction of the œsophagus, stomach and at times the small intestine. The results of Steinach I have already mentioned. In view of the different results of Waters and Steinach, it was desirable that the subject should be re-investigated.

The main part of Waters' paper was on the vaso-motor nerves to the viscera. In the course of his work, however, he found that a strong stimulus applied to 3rd, 4th, 5th and 6th nerves, at their exit from the spinal canal led to contraction of the upper portions of the alimentary tract, the 3rd nerve supplying the œsophagus and the lower nerves the stomach and at times the small intestine. My experiments in the earlier part of this paper convinced me that the posterior roots of these nerves contained no efferent fibres to the viscera, and I therefore merely examined the anterior roots for the purpose of discovering whether efferent fibres left the cord in this region for the viscera.

[1] This *Journal*, VI. p. 460. 1885.

My results are negative. The 3rd anterior root was stimulated five times, the 4th seven times, the 5th six times and the 6th four times, without any visible contraction of the œsophagus, stomach and small intestine respectively. There is no difficulty in getting them to contract on stimulating the vagus and I therefore believe that it is the vagus alone that causes contraction of this part of the alimentary canal.

For some time past there has been an increasing body of evidence that, in mammals, the bladder receives fibres from two regions of the spinal cord which are separated from one another, viz. from the upper lumbar region, the fibres passing by way of the sympathetic chain, and from the sacral region, the fibres passing by the nervi errigentes. The question has recently been worked out by Langley and Anderson[1], who find that there is a similar innervation for the lower part of the intestine and the external generative organs.

It is interesting then to ascertain how far a similar arrangement exists in the frog. The existence of fibres corresponding to the nervus errigens (pelvic nerve of Langley and Anderson) is known in the frog. They were demonstrated by Ecker anatomically, and by Gaskell[2], by means of stimulation. Gaskell states that this "cerebro-spinal" supply for the bladder leaves the cord by the 8th and 9th nerves and passes by the nervus errigens to the bladder. I agree with Gaskell as far as the 9th nerve is concerned, but some of the fibres to the bladder also pass out of the cord by the 10th nerve, and except in one case I never got contraction of the bladder on stimulating the anterior root of the 8th nerve. It would seem therefore that the visceral outflow in the pelvic region is by means of the 9th and 10th nerves. That the fibres pass thence to the bladder by the nervus errigens is easily shown by stimulating the 9th and 10th nerves before and after section of the nervus errigens. After section, stimulation of the 9th and 10th nerves will no longer cause contraction of the bladder. Besides this sacral outflow to the bladder, the 7th nerve also contains motor fibres for the same viscus. This fact was previously shown by Gaskell, and I agree with him in saying that the fibres from the 7th nerve to the bladder pass by the rami communicantes and not by the nervus errigens: in three experiments I stimulated the 7th anterior root, after section of the nervus errigens, and got contraction of the bladder as marked as before; but now, on section of the rami communicantes of the 7th nerve, it was impossible to get contraction by even a stronger stimulus applied to the anterior root of the 7th nerve.

[1] This *Journal*, XIX. p. 71. 1895. [2] This *Journal*, VII. p. 26. 1886.

There is then a double nerve supply to the bladder in the frog as in the mammal. The lumbar supply passes out of the cord by the 7th nerve, and the sacral supply by the 9th and 10th nerves. The gap between the two sets corresponds to the 8th nerve. I have stimulated the 7th and 8th anterior roots in 15 cases together and I have got contraction of the bladder in only one instance on stimulating the 8th anterior root. All the other experiments showed a negative result, however strong the stimulus. With the 7th nerve, the result is different; the contraction, it is true, is always much weaker than that caused by stimulation of the 9th and 10th nerves, as was shown by Gaskell, but it is almost always present. In some cases it was slight, and in two cases I could not get it at all; here, however, its place was taken by the 6th nerve. These two latter experiments should be considered as instances of an anterior plexus, the one experiment mentioned above in which I found contraction following stimulation of the 8th nerve, being, on the other hand, a case of posterior plexus.

This result is in accordance with the work of Bidder and Volkmann. They noticed on dissection (although they did not recognise the presence of grey rami) that in the majority of cases, the bundles of fibres from the sympathetic ganglia to the various spinal nerves passed both ways on joining the nerves, some of them running up towards the cord, others turning round to run with the spinal nerves to the periphery. Or, to use the terminology of to-day, the sympathetic bundles consist in most cases of white and grey rami communicantes. This is the case with all the fibres from the 1st to the 7th. *All* the fibres, however, that run to the 8th nerve from the sympathetic ganglion run with the nerve to the periphery; and this is the case also with the 9th nerve. In other words, dissection shows that the 8th and 9th nerves do not contain any white rami, all the sympathetic fibres joining them belonging to the grey set. As the nervi errigentes come from the 9th and 10th nerves only, it follows that all the visceral fibres that leave the 7th nerve must travel to the periphery by the sympathetic system. No visceral fibres leave the cord by the 8th nerve, while those that leave by the 9th and 10th nerves must pass by the nervi errigentes.

These results, then, agree with those gained by stimulation; the contraction of the bladder which follows stimulation of the 7th nerve being abolished by section of the rami communicantes, though it is not affected by section of the nervus errigens, while the reverse is the case with the 9th and 10th nerves: here contraction is abolished by section of the nervus errigens, but not in the least degree by section of the rami communicantes.

The effect on the bladder is bilateral, though rather more strongly marked on the same side than on the opposite.

With regard to the *rectum*, Gaskell[1] stated that there was a double nerve supply similar to that for the bladder. The circular coat was said to be supplied by the "abdominal splanchnics," while the longitudinal coat got its innervation from the "pelvic splanchnics." From my own observations, I think the supply comes entirely from the 9th and 10th nerves. The fibres pass from these nerves to the rectum by the nervi errigentes: in two instances I cut the rami communicantes of the 9th nerve, and then stimulated the anterior root: the contraction of the rectum was not altered at all. Then I cut the nervi errigentes and found the power of contraction had been abolished by the section. There can be no doubt, therefore, that the sacral supply passes to the rectum in the same way as does the innervation for the bladder.

The 8th nerve does not send any fibres to the rectum, nor, I think, does the 7th. I have notes of seven experiments on the anterior root of the 7th nerve, all with a negative result.

The 9th and the 10th nerves supply both coats of the rectum, circular as well as longitudinal. In some cases of posterior plexus the innervation for the rectum comes entirely from the 10th nerve.

The sphincter ani is also supplied by the 9th and 10th nerves; the effect is unilateral and on the same side.

The following table will show at a glance the innervation I have found for the frog's viscera:

Œsophagus		Vagus.
Stomach		Vagus.
Small Intestine		Vagus.
Large Intestine.	(*a*) Upper part	Vagus.
	(*b*) Lower part	9th Anterior Root.
Rectum		9th and 10th Anterior Roots (sometimes only 10th).
Bladder		7th, 9th and 10th Anterior Roots (sometimes only 7th and 9th).
Sphincter Ani		9th and 10th Anterior Roots.

[1] This *Journal*, VII. p. 27. 1886.

SUMMARY.

The following are the chief results to be drawn from this paper:—

1. I am unable to confirm Steinach's assertion that efferent fibres proceed to various parts of the viscera by the posterior roots. They all pass either by the vagus or by the anterior roots.

2. Efferent fibres are, however, present in the posterior roots of the spinal nerves of a limited number of frogs. These efferent fibres pass to the skeletal muscles and not to the viscera.

3. The innervation of the frog is built up on the same plan as is that of the mammal, there being a visceral outflow from the sacral region (9th and 10th nerves) which passes to the bladder by the nervus errigens, and another from the lumbar region (7th nerve) which passes to the bladder by the sympathetic. The gap between the two corresponds to the 8th nerve, which contains no visceral fibres.