THE INNERVATION OF THE PELVIC AND ADJOINING VISCERA.

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PART II. THE BLADDER.

Previous Observations on Efferent Vesical Fibres[1].

As we shall deal almost exclusively with the efferent nerves of the bladder, we omit reference to previous work on its rhythmic contraction, its internal pressure, its afferent nerves[2], and restrict our account of the earlier observations to those which relate to the origin from the spinal cord of the efferent bladder fibres and the course these fibres take.

First as to the upper set of nerves. Gianuzzi, experimenting after the manner of Budge, found that contraction of the bladder in the dog was obtained by pricking the spinal cord at the level of the lower part of the 3rd lumbar vertebra, and that the contraction usually ceased on section of the nerves called later the hypogastric nerves; sometimes in order to stop the effect it was necessary to cut also strands said to run to the bladder from the upper sacral sympathetic ganglia. He concluded that motor fibres ran to the bladder from the lumbar spinal cord, traversing on their way the sympathetic chain and the inferior mesenteric ganglia. The argument is not quite satisfactory, since the absence

[1] Budge. *Virchow's Archiv*, xv. 115. 1858.
Gianuzzi. *Journ. de la Physiol.*, vi. 22. 1863.
Budge. *Zeitsch. f. rat. Med.*, xxi. 1 u. 174. 1864.
Budge. *Pflüger's Archiv*, vi. 306. 1872.
Sokownin. *Pflüger's Archiv*, viii. 600. 1874.
Sokownin. *Jahresberichte* (Hofmann u. Schwalbe), 1877. Abt. ii. p. 87.
H. Nussbaum. *Jahresberichte* (Hofmann u. Schwalbe), 1879. Abt. ii. p. 64.
Langley. *Journ. of Physiol.*, xii. (*Proc. Physiol. Soc.* Dec. 1890).
Navrocki u. Skabitschewsky. *Pflüger's Archiv*, xlviii. 335. 1891.
Sherrington. *Journ. of Physiol.*, xiii. 678. 1892.

[2] We may mention that so far as our experiments go the origin and course of the afferent fibres is the same as that of the efferent fibres of the bladder.

of effect might be due to the progressive decrease in irritability which takes place in the spinal cord after exposure; this explanation seems to be the one adopted by Budge. Sokownin made observations of a similar nature to those of Gianuzzi but did not describe any fibres as passing from the lumbar cord to the bladder except by the hypogastric nerves. He advanced a step by showing that stimulation of the cut peripheral ends of the hypogastric nerves causes contraction of the bladder. H. Nussbaum confirmed Sokownin except that he found that some fibres continued on in the sympathetic chain. This was a return to Gianuzzi's view but with less definiteness as to the course taken by the fibres. Langley stimulated the sympathetic chain from above downwards, taking precautions against reflexes from the spinal cord; he found in the rabbit contraction of the bladder on stimulating the sympathetic from about the 2nd to the 6th lumbar ganglia; indicating that the motor fibres of the bladder arise from about the 1st to the 5th lumbar nerves. The branches from the sympathetic to the inferior mesenteric ganglia also gave contraction. Navrocki and Skabitschewsky stimulated in the cat the lumbar nerves in the vertebral canal and found contraction of the bladder from the 4th and 5th lumbar nerves. They found no effect after section of the hypogastric nerves, and no effect on stimulating the sympathetic a little above the sacral region. Sherrington, in the cat found contraction of the bladder on stimulating the 3rd lumbar nerve, as well as the 4th and 5th, and in two cases out of seven, he obtained a slight effect also on stimulating the 2nd lumbar nerve. In the monkey he obtained contraction from the 2nd, 3rd and 4th lumbar in eight cases, and from the 3rd, 4th and 5th in one case. It will be seen, that the points which require further elucidation with regard to the upper set of nerves are (1) whether two, three or more lumbar nerves have efferent fibres for the bladder, (2) how far these vary in different animals of the same species in correspondence with the anterior, median and posterior arrangement of the spinal nerves, (3) whether any of the fibres take a course other than that of the hypogastric nerves, and if so what exactly the course is.

Passing now to the lower set of nerves. Gianuzzi showed that fibres causing strong contraction of the bladder issue from the spinal cord in the sacral nerves running by the nerve now generally called the nervus erigens to the hypogastric (pelvic) plexus. He found that the nervus erigens arose in the dog from three sacral nerves. His statement that these nerves are the 3rd, 4th and 5th sacral we may dismiss as probably due to a desire to correlate the nerves of the dog with those of man.

Budge's concise remark in 1872 that in the dog, the efferent nerves to the bladder are contained in the 1st, 2nd and 3rd sacral nerves is the earliest we need be concerned with. H. Nussbaum found the same to be the case in the cat. He distinguished, however, between the 2nd and 3rd sacral nerves which caused strong contraction of the bladder, and the 1st sacral nerve, which caused a comparatively weak contraction. Langley obtained similar results to Nussbaum as regards the cat and dog; but found that in the rabbit the effective nerves were one segment lower in origin. Sherrington, also, found in the cat, the three sacral nerves to contain efferent fibres for the bladder, but in his experiments, the 2nd sacral nerve had the maximal effect, after this came sometimes the 1st and sometimes the 3rd sacral nerve. His results so far as they went, seemed to show that this variation was in correspondence respectively with an anterior and a posterior arrangement of the spinal nerves. In the monkey, in two experiments out of nine, the 3rd sacral nerve had no effect. Navrocki and Skabitschewsky found efferent fibres for the bladder of the cat in two nerves only, viz., in the 2nd and 3rd sacral nerves.

The Lumbar Nerve Fibres to the Bladder.

Function. The upper set of nerves cause contraction of the whole musculature of the bladder; but the contraction is strongest at the base of the bladder near the entrance of the ureter. These nerves have, in the cat at any rate, little if any effect on the urethra.

Stimulation of the nerves on one side causes contraction of both sides, in consequence of the decussation of fibres in the inferior mesenteric ganglia[1].

The theory that the lumbar nerves cause contraction of the circular coat and not of the longitudinal coat is untenable. It is hardly contested that histologically two separate coats do not exist—a point that has recently been insisted on by Griffiths[2]—for the bundles of longitudinal fibres are obviously continuous with the bundles of oblique and of circular fibres. As regards actual experiment it will be remembered that Gianuzzi described the contraction produced by stimulating the lumbar spinal cord as being of the same kind as, though weaker than, that produced by stimulating the sacral nerves. And both Langley and Griffiths have observed directly contraction of circular and longi-

[1] Langley and Anderson. This *Journal*, xvi. 423. 1894.

[2] Griffiths. *Journal Anat. and Physiol.*, xxv. 540. 1894; xxvi. 60 and 255. 1895.

tudinal muscles on stimulating either the hypogastric nerve or the pelvic nerve (nervus erigens).

We have stimulated sometimes the lumbar nerves in the spinal canal, sometimes the peripheral ends of the hypogastric nerves, and then investigated the contraction of the outer longitudinal bundles of the bladder in three ways.

(1) The muscular coat during its contraction is observed with a hand-lens. The shortening of the longitudinal as well as of the other muscular bundles is readily seen.

(2) One leg of the animal is held up by a clamp in such a way that the bladder—nearly emptied for the purpose—hangs downward, and the urine remaining in it slightly elongates it. On stimulation of the lumbar nerves or of the hypogastrics, the bladder undergoes very obvious shortening. This experiment should be made before exposure to air has caused the bladder to enter into tonic contraction.

(3) The bladder is cut into longitudinal strips. The strips shorten on stimulating the upper set of nerves in any part of their course; the edges of the strips at the same time curl over.

We may mention here that it can be shown in a similar manner that the pelvic nerve (nervus erigens) contains motor fibres for the circularly arranged as well as for the longitudinally arranged muscles of the bladder.

In view of these facts we have not thought it necessary to repeat the experiments of v. Zeissl[1], especially as they are obviously open to an interpretation other than that which he adopts. It can easily be seen, in the conditions of his experiments, that a longitudinal contraction of the basal portion of the bladder would tend to draw the urethra forward and so give the effects he obtained on stimulating the hypogastric nerve; and that a strong contraction, even if it involved the urethra, would tend to widen the urethral orifice, and so give the effects he obtained on stimulating the nervus erigens. Since v. Zeissl's experiments were made on male dogs, the results are complicated by the presence of the prostate gland, which in these animals is close to the bladder.

The contraction of the bladder produced by the lumbar nerves (or hypogastrics) is not strong enough to cause micturition; but this is not peculiar to the lumbar nerves, for one of the sacral nerves is often equally ineffective. Indeed in some cases one of the sacral nerves causes a weaker contraction than is caused by the 4th or 5th lumbar nerve.

[1] v. Zeissl. *Pflüger's Archiv*, LIII. 560. 1893.

Another matter, which is not so clear, is that of the presence of inhibitory fibres for the bladder in the upper set of nerves. The apparent presence of inhibitory fibres in the hypogastrics was noticed by one of us some time ago (L. *op. cit.* 1890). In the experiments indicating their presence, a tube was passed through the urethra into the bladder, and tied in the urethra, and the tube connected with a burette filled with salt solution. On stimulating the peripheral end of the hypogastrics, there was often a fall of the fluid in the burette after a slight transient rise. The same fact was observed by Griffiths about the same time, and in his recent Paper, he states, that in the dog the inhibitory effect is best seen after the bladder has been made to contract by stimulating the nervus erigens; the subsequent relaxation is quickened by stimulating the hypogastrics.

In a considerable number of experiments on the contraction of the bladder in which we used the graphic method, we obtained not infrequently, on stimulating the lumbar nerves or the hypogastrics a fall of the internal pressure of the bladder, considerably greater than the preliminary rise due to contraction. In one or two cases there was barely any rise before the fall of pressure.

On examining the bladder directly however, we could find no satisfactory evidence of the presence of inhibitory nerve fibres in the hypogastrics. A slight flaccidity follows the contraction brought about by the hypogastrics, but we never observed the flaccidity without the contraction, nor any considerable degree of flaccidity. Moreover we were not able to satisfy ourselves that the normal relaxation after sacral stimulation was quickened by stimulating the hypogastric nerves, and they certainly had no obvious inhibitory effect on the bladder when it had become contracted in consequence of exposure to the air. It seemed clear to us that if the hypogastrics contain inhibitory fibres, their action could only be slight, and that a special series of experiments would be necessary to determine definitely whether or no any such fibres exist. We have consequently not gone further into the matter.

The lumbar set of nerves have very little if any effect on the arteries of the bladder. Occasionally, the hypogastrics seemed to give slight constriction of the small arteries and slight pallor: but in most cases there is undoubtedly no effect. The small arteries do not contract and the pulsation in them is seen in undiminished extent. The result is the more striking since the small arteries of the intestine, of the uterus, and of the penis, on stimulation of the upper set of nerves take ordinarily but a few seconds to disappear completely from view.

Origin. In the following Table we give the results of our experiments as to the lumbar nerves which cause contraction of the bladder. The symbols S. M. etc. are used with the same meaning as in earlier Tables (cf. Part I. p. 84).

Course taken by the lumbar nerve fibres. In a considerable number of cases we have found no effect on the bladder from stimulation of the lumbar sympathetic or of the lumbar spinal nerves, after the hypogastric nerves have been cut. But sometimes a slight contraction is still obtained. In most cases the fibres which cause this contraction run to the pelvic plexus from the aortic plexus or from about the region of the 6th lumbar ganglion. For it is rare to obtain contraction of the bladder either in cat or rabbit, by stimulating the sympathetic at or below the 7th lumbar ganglion. Since however this does occur occasionally—and we give an instance of it in Protocol II.—we conclude that a few fibres for the bladder occasionally leave the sympathetic for the pelvic plexus as low down as the 1st sacral ganglion.

We have said[1] that in the cat, the hypogastric nerve commonly divides into two strands, the smaller and more dorsal we have called the accessory hypogastric. Sometimes the division takes place close to the inferior mesenteric ganglion; when this variation occurs, it is easy to determine that the larger strand, the hypogastric proper, supplies chiefly the bladder and the uterus (or vas deferens), and that the accessory hypogastric supplies chiefly the rectum and internal anal sphincter. In one or two cases the accessory hypogastric has had no effect at all on the bladder. An instance of this is given in the following Protocol of an experiment.

Protocol II.[2] *Cat. Stimulation of the pudic nerve, of the sympathetic trunk after section of the pudic, of the hypogastric and accessory hypogastric.* Chloroform then A. C. E. mixture by tracheal tube. Tie and cut pudic nerves on both sides.

Stimulate peripheral ends of left pudic nerves. Strong contraction of external anal sphincter and of elevator of scrotum; quick projection of penis, penis soon becomes bluer, then pale and retracts. Contraction of tunica dartos of scrotum.

Tie and cut on both sides the sympathetic chain below the 6th lumbar ganglion, isolate each up to the 7th ganglion. Tie and cut left hypogastric

[1] This *Journal*, XVI. 413. 1894.

[2] In this and in other cases, we select for detailed description an experiment which, in addition to showing the action of the nerves upon the particular viscus we are discussing at the moment, shows also the action of the nerves upon the viscera generally.

Origin of Upper Set of Nerves to the Bladder.

	Dog				Cat									Rabbit					
Exp.		8 11	1 3. 7[1]	4 5	59	21	65	27	63	26	64	20	56	27	37	9	23	32	31
I	Lumbar	—	0	—	—	—	—	0	0	0	—	0	0	0	0	0	—	—	—
II	,,	M	S	—	—	?S	—	?S	0	0	0	0	0	S	0	0	—	—	—
III	,,	**M**	M	—	—	M	—	S	S	?0[2]	S	S	S	M	S.M	S	C	—	—
IV	,,	0	M	M	M	**M**	M	M	**M**	C	M	**M**	M	—	M	C	C	M	—
V	,,	—	0	0	0	0	0	S	S.M	C	S	M	M	—	M	C	C	M	M
VI	,,	—	0	0	0	0	—	—	—	0	0	—	0	—	0	—	0	—	0
Lumbo-sacral Nerves		Ant.	—	4 M to P 5 Post.	Ant.		Med.			Post. (*a*)		Post. (*b*)		Ant.	A to M	M	M to P	P	

M indicates a greater contraction than M.

C ,, that a contraction was observed, but its strength not compared with that from other nerves.

In all of these Exps., except Nos. 20 and 21, the bladder was directly observed. In these two a tracing was taken.

[1] No. 7. Plexus posterior; there were 13 thoracic but only 6 lumbar vertebræ.

[2] The anterior ramus to the inferior mesenteric ganglion was cut.

nerve. On the right side the hypogastric consists of two distinct nerves, the smaller being the 'accessory' hypogastric, tie and cut these separately.

Stim. left sympathetic. No effect seen on penis or scrotum. Strong erection of hairs of tail; this occurred with all later stimulations of the sympathetics. Some contraction of bladder.

Stim. right sympathetic. Effects like those of left, but less contraction of bladder.

Stim. both hypogastrics. Trace of movement of penis; no effect on scrotum, good contraction of vasa deferentia, moderate contraction of bladder.

Stim. accessory hypogastric. No effect on bladder, slight longitudinal and circular contraction at junction of colon and rectum.

Stim. right hypogastric. Contraction of bladder, no certain effect on colon or rectum.

Tie and cut the left nervus erigens, with its accompanying blood vessels, close to the pelvic plexus.

Stim. left sympathetic. No effect seen on bladder.

Stim. right sympathetic. Apparently slight contraction of bladder.

Cut through prepuce, free the penis from surrounding tissue up to limb muscles.

Stim. the medio-posterior branch of the left nervus erigens. Slow enlargement and protrusion of the penis.

Stim. left sympathetic. Slight shrinking of the penis.

Stim. nervus erigens to obtain erection, then

Stim. right sympathetic. Slight shrinking of the penis.

Stim. hypogastrics. Slight further shrinking of the penis.

The Sacral Nerve Fibres to the Bladder.

There are in the dog and rabbit generally three nerves in the sacro-coccygeal region which contain motor fibres for the bladder. In the cat there are three such nerves if the lumbo-sacral plexus is anterior in arrangement, otherwise two only. But so far as our experiments go, two nerves only, are capable in normal conditions of causing micturition. In the cat these are, in nearly all cases, the 2nd and 3rd sacral nerves, and in the rabbit the 3rd and 4th sacral nerves. The contraction produced by the remaining nerve, then, is not sufficiently powerful to cause expulsion of the urine.

We have generally taken note in our experiments whether micturition was produced or not. In giving a brief statement of the results in the cat, we will omit the experiments in which, in addition, the bladder was observed directly. The experiments were 15 in number. The 7th lumbar and 1st coccygeal had no effect in any case. In two

cases (Nos. 6 and 45, Nerves anterior) the 1st and 2nd sacral caused some micturition, the 2nd sacral having the stronger action: in the thirteen other cases, micturition was produced by the 2nd and 3rd sacral nerves only. The arrangement of the lumbo-sacral nerves in these was; anterior in two (Nos. 2, 5), anterior to median in one (No. 32), median in four (Nos. 13, 37, 40, 58), median to posterior in two (Nos. 46, 52), moderately posterior in two (Nos. 39, 44), very posterior in two (Nos. 17, 29).

Although two nerves cause micturition, there is always a more or less marked difference in their action. The anterior of the two nerves, as a rule, produces micturition only after the cessation of the stimulus to the nerve, or after the stimulus has been continued for some time; the posterior one, on the other hand, causes micturition at once, allowing for the ordinary latent period of unstriated muscle. The difference in the effect is due to the fact that the anterior nerve contains efferent fibres for the striated muscles of the urethra and generative organs, whilst the posterior does not. On giving curari, or on cutting the pudic nerves, the difference is no longer seen. And in such case micturition *may* be produced, though it usually is not, by the remaining of the three nerves which contain efferent fibres for the bladder.

In the rabbit when there is much resistance, to the outflow of urine, strong contraction of the bladder drives urine into the seminal vesicles (uterus masculinus) or into the muscular upper portion of the vagina. This usually sets up rhythmic contraction of these organs. The seminal vesicles may drive the urine back again, though usually incompletely. Sometimes raising the lower part of the body by the tail compresses the urethra sufficiently to produce this result.

When the sacral nerves are repeatedly stimulated, and the bladder is not allowed to empty itself, it becomes less responsive, and thus a nerve which at the beginning of an experiment caused a slight contraction, may later produce none.

We have not been able to satisfy ourselves that the sacral nerves have any action on the vesical arteries. When they cause strong contraction there is great pallor of the bladder, but this may be merely a mechanical effect. When the contraction is greatly diminished by a large dose of atropin (cp. below p. 82) the sacral nerves have still no obvious vaso-motor action.

Unilateral action of the sacral nerves. Gianuzzi mentioned that the sacral nerves of one side caused contraction chiefly of the same side of the bladder, but he does not appear to have given any close attention

to the matter. According to Griffiths and to Sherrington the action of these nerves is strictly unilateral. We have made a few observations on the rabbit and cat and we do not find a strictly unilateral action. In our observations we cut through the bladder in the middle line, a variable distance from the tip towards the opening of the ureters. We then stimulated on one side one or more of the carefully isolated sacral nerves, or the pelvic nerve (nervus erigens) near its origin. In five cases out of six there was distinct, though in most cases slight, contraction in the part of the bladder on the opposite side which had been separated by the cut from its fellow portion: and this occurred whether the bladder on the same side was allowed free movement, or clamped at its tip in order as far as possible to prevent movement. If the bladder be not emptied, then as described by Griffiths, the half on the stimulated side contracts, whilst the opposite side is bulged out.

Origin. We give below, the experiments we have made upon the origin of the sacral nerve fibres to the bladder. It will be seen that our results as regards the cat explain most of the discrepances in earlier results; thus Nussbaum probably experimented with cats in which the arrangement of nerves was anterior, and Navrocki with cats in which the arrangement was posterior. It is true, that Sherrington describes the 1st sacral as giving sometimes a stronger contraction than the 3rd sacral; this we have not found, but it is perhaps possible that in his cases the nerves were arranged more anteriorly than in any of those marked 'Anterior' in our Table of Experiments.

Origin in Rabbit of Lower Set of Nerves to the Bladder.

Exp.	13	37	30	29	$\frac{4}{20}$	36	32	22	$\frac{21}{28}$	10	$\frac{33}{34}$	31
I Sacral	0	0	0	0	—	0	—	0	0	0	0	0
II ,,	G	S	0	?S	—	0	—	0	0	0	0	0
III ,,	G	G	G	G	G	G	G	G	G	G	G	M
IV ,,	S	G	—	S.M	G	G	G	G	G	G	G	G
I Coccygeal	0	0	—	0	?0	S	—	—	S	S	M	M
II ,,	—	—	—	—	—	—	—	—	0	—	0	0
	A	A to M	Med. to Ant. (about)		—	M to P	Posterior					

Origin in Cat and Dog of Lower Set of Nerves to the Bladder.

	Cat													Dog			
Exp.	19 24	57[1] 59	21[2] 22		60 63	62	16	49 61	53	54	50 55	64	56	6 2	4	5	7[3]
VII Lumbar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I Sacral	S.M	S	C	S	S	0	0	0	0	0	0	0	0	S.M	0	0	0
II ,,	G	G	C	G	G	G	G	G	G	G	G	G	G	G	G	G	G
III ,,	—	G	C	G	G	G	G	G	G	G	G	G	G	G	G	G	G
I Coccygeal	—	0	0	0	0	0	0	0	0	0	0	0	0	0	S	S	M
Arrangement of Nerves	Anterior			—	Median		—	Median to Posterior			$P_{(a)}$		$P_{(b)}$	6 Ant. 2 A to M	M to P	Post.	

[1] Cat had 14 thoracic nerves.

[2] Relative degree of contraction of I S. and III S. not noted.

[3] There were only 6 lumbar nerves.

Note on the action of some alkaloids. When a tracing of the internal pressure of the bladder is taken, it is seen that intravascular injection of a small quantity of nicotin causes, first a strong contraction, and subsequently a very considerable dilation. Curari usually causes a moderate primary contraction. The effect of atropin on the tone of the bladder we have not noticed; a moderate dose has very little action upon the effectiveness of the efferent nerves. A large dose weakens the contraction produced by nerve stimulation; thus in an experiment on a dog 150 mgrms. of atropin were injected into the jugular vein; then stimulation of the 1st sacral nerve—which previously had caused distinct though slight contraction—had no effect, strong contraction was however produced by stimulation of the 2nd and 3rd sacral nerves. A further injection of 100 mgrms. was made; the 2nd and 3rd sacral nerves still had an effect, though comparatively slight; the contraction also was transient, occurring at the beginning of the period of stimulation and rapidly disappearing. In the rabbit and cat 50 mgrms. is the maximum amount we have injected; the contraction of the bladder from nerve stimulation was weakened, but to the eye, not very greatly.

Summary.

The results which we have obtained as to the origin and course of the efferent fibres to the bladder are in large part simply confirmatory of facts which have been already shown by some one or other observer. (Gianuzzi, Budge, Sokownin, H. Nussbaum, Langley, Navrocki and Skabitschewsky, Sherrington.) But we have been able to give more definiteness to the account, by explaining the discrepancies which exist in the previous statements. The discrepancies are due, as a rule, to the experiments having been insufficient in number, so that the variations which occur in different individuals escaped notice.

The slight, and somewhat variable effect, which the lumbar nerves have on the bladder, makes it difficult to determine with any exactness their relative efficiency. And, in consequence, we have not always found such marked variations to exist in the lumbar innervation of the bladder according to the arrangement of the lumbar nerves, as we have found in other cases. But the details we have given on p. 77, afford we think some evidence of the following scheme of innervation.

	Dog		Cat			Rabbit	
	Anterior	Posterior	Anterior	Median	Posterior	Anterior	Posterior
II L.	Moderate	Slight	? Slight	0	0	Slight	0
III L.	**Moderate**	Moderate	Moderate	Slight	Slight	Moderate	Slight
IV L.	0	Moderate	**Moderate**	**Moderate**	**Moderate**	**Moderate**	Moderate
V L.	0	0	0	Sl. to Mod.	Moderate	Moderate	Moderate
VI L.	0	0	0	0	0	0	0

It will be noticed that the origin of the nerves to the bladder is more anterior in the dog than in the cat. This is probably connected with the greater development of nerves to the hind limb.

The variations in sacral nerve supply work out with greater certainty. They are

	Cat		Dog		Rabbit	
	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior
VII L.	0	0	0	0	0	0
I S.	Sl. to Mod.	0	Sl. to Mod.	0	0	0
II S.	**Good**	Good[2]	Good	Good	Sl. to Mod.	0
III S.	Good	Good[2]	Good	**Good**	**Good**	Good
IV[1]	0	0	0	Sl. to Mod.	Mod. to Good	**Good**
V[1]	0	0	0	0	0	Sl. to Mod.

[1] We have, for simplicity, numbered these from the 1st sacral downwards; IV is the 1st coccygeal in the cat and dog; V is the 1st coccygeal in the rabbit.

[2] Sometimes one, sometimes the other appears to have the maximum effect.

We have omitted in this scheme the median arrangement of nerves; this is intermediate between the anterior and posterior, and the sacral innervation of the bladder inclines towards that occurring with an anterior or a posterior plexus, according as the plexus itself is on the anterior or posterior side of median.

It will be noticed that in the dog the 1st coccygeal nerve sends fibres to the bladder when the plexus is posterior, and that this is not the case in the cat. This is probably due, like the similar difference in the lumbar innervation, to the greater development of nerve fibres for the hind limb in the former animal.

Comparing the origin of the nerve fibres for the bladder with the origin of the nerve fibres for the descending colon and rectum—described in Part I.—we see that the difference is slight. So far as our experiments go, the bladder does not receive efferent fibres from the 13th thoracic or 1st lumbar nerves, and comparatively seldom from the 2nd lumbar. Thus the bladder appears to be supplied with efferent fibres by fewer lumbar nerves than the descending colon, rectum, and

internal anal sphincter. But as the effect produced by a given lumbar nerve is considerably greater on the end of the intestine than on the bladder, it is possible that the two viscera may be supplied by the same nerves, but that the upper lumbar nerves are only capable of causing a contraction of the bladder in exceptionally favourable circumstances.

A few lumbar fibres occasionally pass to the pelvic plexus and so to the bladder,—as has been described by Gianuzzi and Nussbaum—without traversing the inferior mesenteric ganglia and hypogastric nerves. The accessory hypogastric, when it occurs, contains few or no fibres for the bladder.

We give some additional—and we think conclusive—evidence for the view that both the lumbar nerves and the sacral nerves cause contraction of all the muscle fibres of the bladder, whether they are circular, oblique or longitudinal. Inhibitory fibres for the bladder are few, if indeed any exist.

The vesical arteries do not, as a rule at any rate, receive either constrictor or dilator fibres from the lumbar nerves; nor is there satisfactory evidence that they receive vaso-motor fibres from the sacral nerves. Micturition, normally, is only produced by two nerves out of the five to seven which have efferent vesical fibres. These are in nearly all cases the 2nd and 3rd sacral in the cat and dog, and the 3rd and 4th in the rabbit; the anterior of these two nerves only causes micturition on the cessation of the stimulus, since it causes also contraction of the striated muscles of the genito-anal apparatus.

The lumbar nerves have a bilateral action on the bladder owing to a decussation of fibres in the inferior mesenteric ganglia.

The sacral nerves have also a bilateral action, though the contraction on the side of the bladder opposite to the nerve stimulated is very slight compared with the contraction on the same side. The stimulus here probably spreads directly through the plexus of unstriated muscle.

PART III. THE EXTERNAL GENERATIVE ORGANS.

CONTENTS.

THE parts of the generative organs with which we are concerned here are those developed from the uro-genital sinus and the skin surrounding the uro-genital opening. In the male these parts are the penis, the scrotum, and in some cases other parts of the skin in the genital region. In the female, they are the vulva and the genital skin; in the term vulva is included the vestibule stretching a short distance above the urethral opening. In human anatomy the vagina is commonly included in the external generative organs. It is well known, however, that developmentally it belongs to the internal generative organs, and we shall show later that it belongs to them also by its innervation.

PREVIOUS OBSERVATIONS[1].

Eckhard was the first to show that certain nerves when stimulated cause enlargement of, and increase of blood-flow through, the penis.

[1] See Foot-note on the next page.

These nerves he called the nervi erigentes. He found by dissection that in the dog they arose from the 1st and 2nd sacral nerves, and occasionally from the 3rd sacral nerve also. The experiments of Goltz showed the existence of an erector centre in the lumbo-sacral region of the spinal cord. Gaskell determined that the erector fibres left the spinal cord by the anterior and not the posterior roots, and in the rabbit by the anterior roots of the 2nd and 3rd sacral nerves. In the dog, Morat found them in the anterior roots of the 1st and 2nd sacral nerves. Langley described stimulation of the sacral nerves in the vertebral canal as producing sometimes dilation and flushing, sometimes contraction and pallor of the vagina (vulva). In the rabbit the former effects were most prominent with the 3rd and 4th sacral nerves, the latter with the 1st and 2nd sacral. The innervation of the penis was the same as that of the vulva; the sacral nerves causing either protrusion and flushing of the penis, or retraction and pallor. Sherrington observed in the monkey contraction of the external sphincter of the vagina on stimulating the 2nd and 3rd sacral nerves, the 3rd had usually a greater effect than the 2nd. The 1st sacral gave no certain result, but in three experiments out of sixteen it may have caused some contraction. In two experiments on the male, the 2nd and 3rd sacral nerves produced moderate, and the 1st sacral slight erection. In the cat, strong contraction of the external sphincter of the vagina was produced by the 1st and 2nd sacral, the 2nd giving usually a rather greater effect than the 1st. He states also that turgidity was produced by the 1st and 2nd sacral, and slight turgidity by the 7th lumbar nerve. Nikolski differed from Eckhard as to the result obtained by excitation of the anterior ramus of the nervus erigens in the dog, i.e. the ramus from the 1st sacral nerve. He found a vaso-constrictor, instead of a vaso-dilator effect. François-Franck states that this ramus is capable of producing either action.

[1] Eckhard. *Beiträge zur Anat. u. Physiol.* III. 123. 1863. (This Article gives an account of earlier observations); IV. 69. 1869; VII. 67, 115, 196. 1876.
Goltz. *Arch. f. d. ges. Physiol.* VIII. 460. 1874.
Nikolski. *Arch. f.* (*Anat. u.*) *Physiol.* 1879. 209.
Gaskell. *Journ. of Physiol.* VII. 1. 1886.
Gaskell. *Proc. Physiol. Soc.* Jan. 1887. (*Journ. of Physiol.* VIII.)
Morat. *Arch. de Physiol. norm. et path.* 1890.
Langley. *Proc. Physiol. Soc.* Dec. 1890. (*Journ. of Physiol.* XII. 1891.)
Sherrington. *Journ. of Physiol.* XIII. 675, 686. 1892.
Langley and Anderson. *Journ. of Physiol.* XVI. 417. 1894.
François-Franck. *Arch. de Physiol. norm. et path.* 1895, 122, 138.

Eckhard described erection as being produced in the rabbit, but not in the dog, by stimulation of the hypogastric nerves. Langley and Langley and Anderson found that these nerves sometimes contained constrictor fibres for the external generative organs. The fibres arose from the lumbar nerve-roots—about the 2nd to the 5th. François-Franck in the dog noticed chiefly a vaso-dilator effect on the vessels of the penis on stimulating the hypogastric nerves, but occasionally a vaso-constrictor effect was produced. Some of the branches running from the sympathetic to the inferior mesenteric ganglion had a similar effect.

Vaso-constrictor fibres for the penis were found by Eckhard in the nervus dorsalis penis. Gaskell suggested that the n. pudendus communis received its vaso-motor fibres from the grey rami of the sympathetic ganglia. Langley found constrictor fibres for the external generative organs of the male and female to arise from the lumbar spinal cord. The fibres—except a few going to the hypogastric nerves—ran down the sympathetic to the sacral ganglia, there became connected with nerve-cells and continued their course first in the grey rami of the ganglia and then in the sacral nerves.

The Upper Set of Nerves in the Male.

The general effects of stimulating the upper set of nerves are the same in the rabbit, the cat, and the dog. And in all cases unilateral stimulation has a bilateral visceral effect, though the effect is greater on the stimulated side. The effects are:

1. *Contraction of blood vessels.* The contraction of the arteries of the penis, both large and small, is very great. This is most readily seen in the dog; the large arteries which run on either side of the body of the penis contract to such an extent that the pulse in them disappears. The contraction of the arteries causes, of course, pallor, and decrease in size of the penis, varying according to the state of distension at the time.

There is also some contraction of the arteries of the whole genital skin. In the rabbit, the vessels in the median surface of the scrotum are clearly seen through the skin. On stimulating the upper set of nerves, the skin becomes slowly quite pale. In the rest of the genital skin of the rabbit, and in the whole region in the cat, the vessels are only imperfectly or not at all seen. But if the skin be cut, the blood-flow may be made slower by stimulating the upper set of nerves. The

contraction of the skin vessels is much less prompt than that of the vessels of the penis; and the upper lumbar nerves often have no visible effect upon the skin vessels, though causing distinct pallor of the penis.

2. *Contraction of the retractor muscle of the penis.* This muscle is well known in many animals; a sketch of it in the dog has been given by Eckhard (*op. cit.* 1863), who speaks of it as the 'Afterruthenband.' It is a thin band of longitudinally arranged unstriated muscle (15 to 20 centimetres long in a spaniel, weighing about 15 kilos), inserted at the attachment of the prepuce, and continued backwards in the middle line over the ventral surface of the corpus spongiosum and bulbus urethræ. In this part of its course the retractor runs in a loosely attached sheath, and is apparently a single strip of muscle, though easily divided into two halves near the bulb. Two small slips of the bulbo-cavernosus muscles in the dog accompany the retractor for the distance of 2 to 3 centimetres towards its insertion, and then join ventrally, forming a sling through which the retractor passes. Behind the bulb the muscle divides into two slips which pierce the external sphincter of the anus, passing one on either side of the gut; some of the fibres of either slip are continuous with a portion of the caudo-cavernosus muscle of the same side, others are attached to the urethra immediately behind the bulb, and a few pass dorsally to the urethra in the recto-urethral septum and may be traced as far as the prostate (see Fig. 1). The connection between the retractor and the caudo-cavernosus muscle is not easily seen in the dog but is obvious in the cat.

A few striated muscle fibres are found in the retractor in the cat and dog; they are derived chiefly from the external sphincter of the anus, but a few fibres probably pass into the retractor from the bulbo-cavernosus muscles.

The retractor muscle is well adapted for determining which lumbar nerves have an effect on the penis; it is exposed by a simple skin incision, and its contraction is easily seen. With a little care, the circulation of blood in it can be seen under the microscope; the vessels become nearly empty on stimulation of the lumbar sympathetic or of (e.g.) the 3rd lumbar spinal nerve. Further, it may be cut at its insertion and freed from the corpus spongiosum; and thus a long slip of muscle obtained connected only at its base. The slip contracts powerfully on stimulating the upper set of nerves. The fibres from these nerves run to the muscle, chiefly, at any rate, by way of the nervus dorsalis penis. In the *cat* the retractor muscle is more embedded in connective tissue than it is in the dog, and

until dissected out, it is seen in outline only. When it contracts it causes a marked dorsal curving of the penis. In the *rabbit*

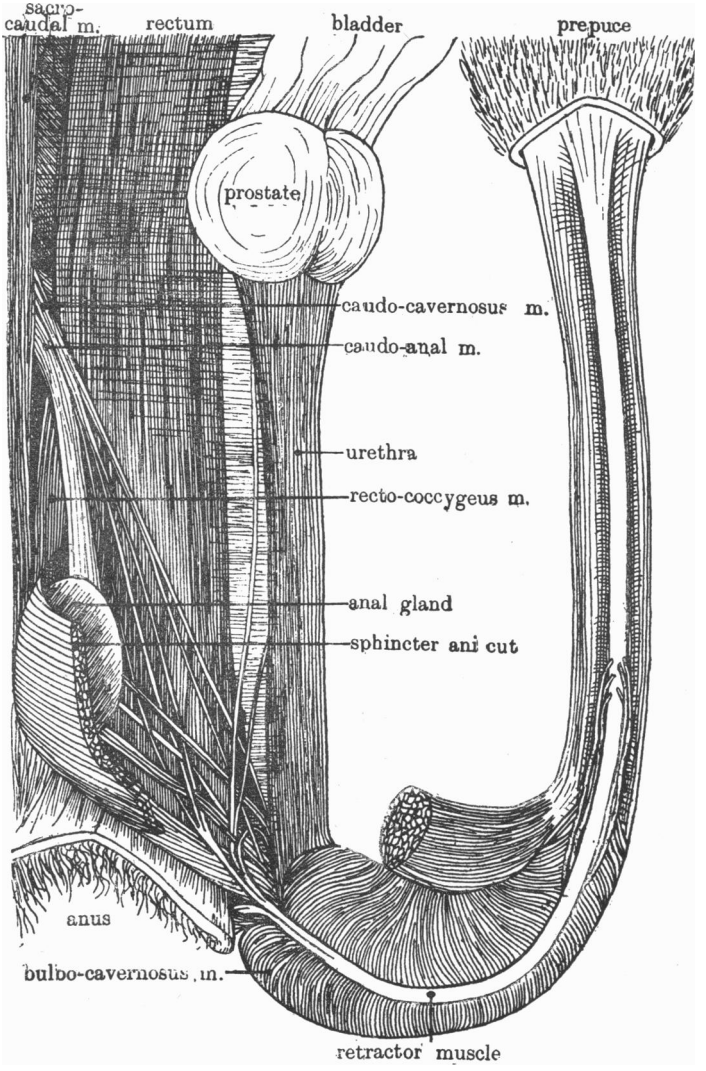

FIG. 1.

Course and connections of the Retractor Penis of the Dog. Natural size.

there is no obvious muscle homologous with the retractor in the dog and cat.

It will be convenient to describe here some other unstriated muscles of the genito-anal region.

Frankenhaüser[1] indicates in Fig. 2 Pl. II. a muscle in the rabbit called by him the 'attractor' recti: this muscle arises from the 1st coccygeal vertebra between the two sacro-caudal muscles (m. flexores caudæ of Krause), and at its origin is composed of a single thin layer of unstriped muscle, which soon divides into two portions, homologous with the caudo-cavernosus and caudo-analis muscles described and drawn by Straus-Dürckheim[2] in the cat. In the cat and dog these muscles arise as in the rabbit between the sacro-caudal muscles as a single thin layer composed of unstriped fibres, but from the 2nd coccygeal vertebra. The anterior portion, forming the caudo-cavernosus muscle, is partly attached to the bulb and partly continued into the retractor penis; the lower portion, forming the caudo-analis muscle, passes under the external sphincter of the anus, and is attached to the anal skin. In the rabbit, the caudo-cavernosus muscle is very slight, and passes to the prepuce; the caudo-analis muscle, however, is well marked and distributed to the anal skin. The unstriped muscles of the genito-anal skin are also connected in the rabbit with a strong band of unstriped muscle, which extends from the urethral bulb to the seminal vesicles, running in the recto-urethral septum.

3. *Contraction of the intrinsic muscles of the penis.* In the cat and rabbit, when the body of the penis is cut open, it is seen that its whole musculature contracts on stimulation of the lumbar set of nerves. Retraction is thus produced when there is no blood-flow through the penis and in the cat when the retractor muscle has been cut away. The movement brought about by the contraction of the blood vessels, of the intrinsic muscles of the penis, and of the retractor muscle, working together, is considerable, and is conspicuous on external observation.

In the dog, the upper set of nerves cause slow movements in the penis itself, apart from that caused by the retractor muscle, but to these we have not paid much attention; the most obvious movement is the shrinking of bulbus urethræ. Externally very little change is seen in the dog after paralysis of the striated muscles: the thick skin hiding the effects which occur.

4. *Contraction of the unstriated muscles of the genital skin.* This corresponds with the contraction of the anal skin, which we have

[1] *Jenaische Zeitschr. für Medicin*, II. 1866.

[2] *Anatomie du Chat.* (Paris), 1845, pp. 319, 326.

mentioned in Part I. It is marked in the rabbit, much less in the cat, and slight only or absent in the dog. In the rabbit, the body of the penis lies underneath the end of the rectum, and both project from the limb muscles—an arrangement which does not exist in the cat or dog; the two or three centimetres of skin which cover the body of the penis move dorsally and anteriorly on stimulation of the lumbar set of nerves.

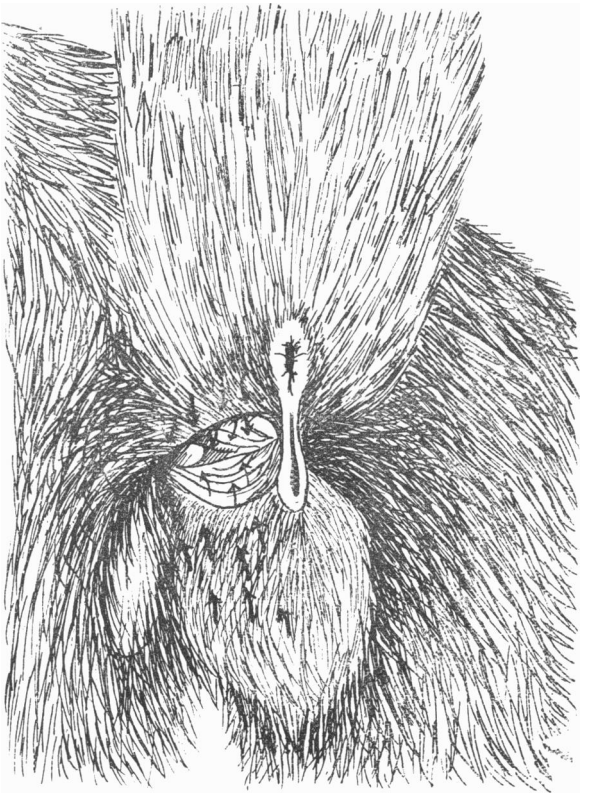

FIG. 2.

Diagram to show movement of genito-anal skin muscles in the rabbit produced by stimulating the upper set of nerves.

The skin over the end of the rectum moves at the same time ventrally and anteriorly, thus the body of the penis and the end of the rectum are brought nearer together along their whole length (cp. Fig. 2). With this there is contraction of the prepuce, which moves a little posteriorly, and closes over the retracting penis. The movement

of the prepuce may be distinct, when the penis, being already small, undergoes no further retraction. In the cat, there is contraction of the prepuce and a less obvious movement of the skin towards the anus.

5. *Contraction of the scrotum.* This comes under the previous section, but it is convenient to mention it separately. The movement in the rabbit is slight, and easily overlooked; it is obvious in the cat and dog, causing strong puckering of the skin. It must be remembered that some movement in the rabbit (less in the cat) may be caused by contraction of the vas deferens, and strong movement in the dog by contraction of the cremaster. Here of course we are only dealing with movement caused by contraction of the skin muscles (tunica dartos).

6. *Contraction of the cremaster.* Since this muscle does not belong to the visceral system, we have not paid very much attention to it. And we will give at once the results we have obtained as to the origin and course of the nerve fibres supplying it. First we should mention that Sherrington (*op. cit.* p. 683) found in Rhesus that the cremasteric muscle was innervated by the 2nd and 3rd lumbar nerves in eight cases and by the 3rd and 4th lumbar nerves in one case. In the cat and rabbit we have not seen any cremasteric contraction on stimulating either the lumbar spinal nerves or the genito-crural. And microscopic sections of the spermatic cord do not show the presence of any striated muscle. We conclude that in the cat and rabbit the cremaster is absent. In the dog we have made experiments with the results given in the following Table:

Origin of Nerves to Cremaster in Dog.

Exp.	$\frac{8}{11}$	10	4	7	5
I Lumbar	0	—	—	0	—
II ,,	0	—	—	0	—
III ,,	G	G	—	0	—
IV ,,	0	0	G	G	—
V ,,	—	0	0	0	0
Arrangement of Nerves	Markedly anterior	Med.[1]	Med.[1]	Post. (*a*)	Post. (*b*)[2]

[1] No. 10 was a little above and No. 4 was a little below the strictly median type.
[2] 6 Lumbar nerves only, the nerve below the 13th thoracic is in this Table counted as the 2nd lumbar, and the 13th thoracic as the 1st lumbar.

G indicates a good contraction.

It will be noticed that in Exps. 7, 8 and 11 at least, the cremaster received its motor fibres from a single nerve, either from the 3rd lumbar nerve or from the 4th. It is however possible that with a strictly median arrangement of nerves, the nerve fibres for the cremaster may be divided between the 3rd and 4th lumbar nerves.

Since the scrotal contraction is strong in the dog, it is possible, though not very excusable, to mistake it for the cremasteric contraction. Hence it is advisable to lay bare the spermatic cord near the epididymis, and hold it between finger and thumb; the contraction of the cremaster is then easily felt.

Unilateral stimulation gives unilateral contraction of the cremaster, the fibres run in the genital branch of the genito-crural nerve. We may mention that the genito-crural nerve contains non-medullated nerve fibres, but we have not seen any visceral effect on stimulating its peripheral end, either in the dog, cat or rabbit.

We have not found any satisfactory evidence of the presence in the lumbar nerves of vaso-dilator or inhibitory nerve fibres for the external generative organs, either in the male or female. We have found once or twice, as one of us found earlier, a slight flushing of the penis or vulva on stimulation of the upper lumbar nerves, and of the upper part of the lumbar sympathetic, but we are inclined after repeated experiments, to attribute the rare flushing to other causes than a stimulation of vaso-dilator fibres. On this point we shall later say something more.

After section of the lumbar nerves, or after section of the lumbar sympathetic in its lower region, there is usually more or less erection; obviously owing to a removal of tonic impulses to the arteries and unstriated muscle of the external generative organs.

Origin from the Spinal Cord. In the rabbit we have made a considerable number of experiments, stimulating the sympathetic trunk from above downwards (cp. Part I. p. 78). Sometimes there was a slight effect on stimulating just below the 2nd lumbar ganglion; a distinct though still weak effect was commonly obtained on stimulating below the 3rd lumbar ganglion; the effect was greater below the 4th, and greater again below the 5th lumbar ganglion. From this point down to the end of the sacral region, differences in the degree of action were difficult to determine. These experiments showed that constrictor nerves for the external generative organs commonly arise from the 2nd, 3rd and 4th (and possibly lower) lumbar nerves, and occasionally from

the 1st lumbar nerve also. Some similar experiments were made in the cat and with similar results.

We have also made more direct observations by stimulating the lower thoracic and the lumbar nerves in the vertebral canal. The results of these experiments we give in the Table on page 95. The symbols S. M. etc. are used with the same meaning as in earlier Tables (cp. Part I. p. 84). Unless otherwise mentioned in the Foot-notes to the Table, the effects observed in the cat and rabbit were, retraction and pallor of the penis, contraction of the skin muscles; and in the cat, contraction of the scrotum also. The body of the penis was not as a rule exposed[1] except in the dog, so that the changes were all observed on the structures visible externally. It may be noted that in these conditions, the upper effective spinal nerves caused slight pallor with little or no contraction of the penis. In the dog, contraction of the exposed retractor muscle, of the dorsal artery, and of the scrotum, were the chief points observed.

Upper Set of Nerves in the Female.

In their nature, the effects produced by the lumbar set of nerves in the female are, *mutatis mutandis*, the same as in the male. They are (1) pallor of the clitoris and of the mucous membrane of the vulva, with slight retraction of the clitoris. (2) Contraction of the vulva. This is much more obvious in the rabbit than in the cat and dog. In the rabbit the contraction is least just inside the vulvar orifice. The contraction of the vulvar orifice itself may be considerable. (3) Contraction of skin muscles, drawing the vulva dorsally. In the cat and dog there is a slight movement only of the vulvar orifice towards the rectum. In the rabbit the skin movement is fairly strong and is similar to that in the male (cp. Fig. 2, p. 91), the vulva being moved dorsally and somewhat anteriorly towards the rectum.

In most cases the effects are distinctly less than in the male, and sometimes they are very slight, especially in the cat and dog.

Our experiments on the effects of stimulating the lumbar nerves gave the results shown in the Table on page 96. In the cat pallor of the mucous membrane was chiefly observed, in the rabbit pallor of the mucous membrane and contraction of the genital skin.

[1] In the cat, it was exposed in Nos. 63, 64; in the rabbit in No. 37.

Origin of Nerves to External Generative Organs in the Male.

		Dog						Cat											Rabbit						
	Exp.	11[1]	8[1]	10	4	7[3]	5	8	3	25[4]	1	32	7	4[5]	63[6]	64[7]	38	11	30	27	37	23	31/32	14	24	26
XII	Thoracic	S	—	—	—	—	—	—	—	—	—	—	0	0	—	—	—	0	0	—	—	—	—	—	—	—
XIII	,,	M	M	—	—	M[2]	—	—	—	—	S[2]	—	?S[2]	?0	—	—	—	S[8]	?0	—	—	—	—	—	—	—
I	Lumbar	S	S.M	—	—		—	—	—	—	S[2]	—	?S[2]	?0	0	—	—	S[8]	?0	0	0	—	—	—	—	—
II	,,	G	G	—	—	M	—	—	S	S	S>I	—	S	C	?0	?S	—	S[8]	?0	S	S	—	—	?S	—	—
III	,,	G	G	G	—	G	—	G	G	M	M	—	G	C	G	M.G	M	S.M	S.M	G	M.G	G	—	S	—	S.
IV	,,	0	0	S.M[2]	G	S.M	—	S	—	M	M	G	M	C	G	G	G	G	G	G	G	G	—	G	G	G
V	,,	0	—	0	0	0	0	—	—	0	0	0	?S	0	M	G	S.M	M	G	—	G	G	G	G	G	G
VI	,,							—	—	—	0	0	0	0	—	—	—	0	0	—	0	0	—	0	0	—
	Arrangement of Nerves		Ant.	Med.	Med.	Post. (*a*)	Post. (*b*)				Anterior		Ant. to Med.		— Med.	P. (*a*)		Posterior (*b*)		A.	A. to M.	Med. to Post.		Post.		

[1] The XIIth and XIIIth Th. caused contraction of the retractor muscle, some contraction of the preputial artery, little or none of the dorsal artery of the penis, nor of the scrotum.
[2] No effect seen on the scrotum.
[3] Six lumbar nerves only present, the 13th thoracic was counted as the 1st lumbar.
[4] Scrotum not observed. Rami to inferior mesenteric ganglia cut.
[5] The arrangement of the nerves was not sufficiently noted; it was either Ant. to Med. or high Median.
[6] The effect on the penis is here given, the origin of the nerves for the scrotum was different, viz. II L. = M; III L. = G; IV L. = G; V L. = 0.
[7] The effect on the penis is here given, the origin of the nerves to the scrotum was, II L. = ?S; III L. = G; IV L. = G; V L. = Trace.
[8] Pallor only obtained.

S. M indicates that the effect varied from Slight to Moderate; M.G that it varied from Moderate to Good.

Origin of Nerves to External Generative Organs in the Female.

	Cat									Rabbit				
Exp.	2	33	37	27	35	10	14	26	9		35	9	19/20	25
XIII Thoracic	0	0	0	—	?0	?0	—	—	—	XII	0	—	—	—
I Lumbar	?S	?0	?0	0	?0	?S	0	0	?0		0	0	—	—
II ,,	S	S	S	?0	—	M	S	0	S		0	0	—	—
III ,,	S	M	M	C	—	M	S	S	M		M	S	M	—
IV ,,	S	S.M	M	C	—	M.G	M	G	G		G	G	M	G
V ,,	0	0	0	?0	—	0	S	G	—		S	M	—	—
VI ,,	0	0	0	—	—	—	—	0	0		0	—	—	—
Arrangement of nerves	Ant.	Ant. to Med.		Median				P.(*a*)	P.(*b*)		A. to M.	Median		P.

Course taken by the Upper Set of Nerve Fibres.

The course taken by the lumbar nerve fibres to the external generative organs is the same in the male and female, but since the effects are generally much more obvious in the male than in the female, we have taken the former in nearly all cases when comparatively slight effects were to be observed. The results given in this section refer to both rabbit and cat unless otherwise mentioned.

The nerve fibres pass from the spinal nerves by the white rami and run to the lumbar sympathetic chain. Stimulation of the sympathetic just above the 1st sacral ganglion produces maximal effects. An experiment bearing on this point has been given in Part I. p. 79. When both sympathetics are cut just above the 1st sacral ganglia, stimulation of the lumbar nerves has a comparatively slight effect; often, indeed, unless special precautions are taken, no effect is to be seen. Hence the great majority of the upper set of fibres run to the external generative organs by way of the sacral sympathetic chain.

Course by pudic nerves. It is equally clear that the great majority of the fibres leave the sympathetic chain by the grey rami of the sacral ganglia, run to the sacral nerves, and reach the periphery by way of the dorsal nerves of the penis or clitoris, the genito-anal and the scrotal nerves. This can be shown in several ways.

(*a*) The sympathetic may be cut above and below each sacral ganglion and the piece of nerve above the ganglion, the ganglion, or the grey ramus itself, stimulated. Proceeding in this way, we have obtained retraction of the penis, and contraction of the tunica dartos from the 1st, 2nd and 3rd sacral ganglia in the cat and dog, and from the 2nd, 3rd and 4th

sacral and 1st coccygeal ganglia in the rabbit. This method is troublesome and we have not attempted to determine by it, the variations in distribution which correspond with the anterior, median, and posterior arrangements of the spinal nerves.

(*b*) The grey rami of the sacral and coccygeal ganglia may be cut, and the sympathetics stimulated just above the 1st sacral ganglia. Such stimulation gives either no effect or a very slight one. This method is still more troublesome than the first, and a considerable reduction of the normal blood flow through the external generative organs is unavoidable.

(*c*) The pudic nerves may be cut and the sympathetics stimulated as in the previous case. Little or no effect is then produced. When all the branches of the pudic nerve are cut on one side, say the right, and the sympathetic on the same side is stimulated, there is still some action on the external generative organs, though more or less confined to the left side. The bilateral action is due to the connection which exists in the sacral region between the sympathetic trunk on the two sides. The lumbar fibres, which descend the sympathetic on one side, run in part to the sacral ganglia of the opposite side.

By a trifling modification of method (*c*), the distribution of the sympathetic fibres contained in each branch of the pudic nerve can be determined. Instead of cutting all the branches at once, they are cut in succession; the sympathetic being stimulated after each branch is cut. We have not worked this out in detail, but in the experiments made the results were as follows:

In the rabbit, section of the nervus dorsalis penis or clitoridis on both sides abolished the effects of the sympathetic on the penis (or clitoris and vulvar mucous membrane) and greatly diminished the effect on the prepuce; section of the superficial genito-anal nerve had no appreciable effect; section of the deep genito-anal decreased greatly the effect on the anal and genital skin.

In the cat after section of the combined nervus dorsalis penis and genito-anal nerve, stimulation of the sympathetic had little or no effect on the penis or skin; but still had a strong effect on the scrotum; after section of the perineal, or simply of the scrotal branches, the sympathetic had no effect on the scrotum.

Course by hypogastric nerves. A certain number of the upper set of fibres—comparatively very few—run to the generative organs by way of the hypogastric nerves. We have said that sometimes slight retraction and pallor of the penis are obtained by stimulation of the lumbar spinal

nerves after both sympathetic trunks have been cut just above the 7th lumbar ganglion. There may be a slight effect on the prepuce, but we have not seen any effect in the skin elsewhere, including that of the scrotum.

Stimulation of the peripheral end of one or of both hypogastric nerves, generally causes some retraction and pallor of the penis, and, if the penis be cut across, some decrease in blood flow. The effect is very variable in extent. In not a few cases, we have found no obvious effect; but in these cases, the body of the penis was not exposed and its blood vessels were already moderately contracted. In all doubtful cases it is advisable to expose the body of the penis, and to stimulate the genital branch of the nervus erigens before stimulating the hypogastrics. Very marked effects may then be observed. The hypogastrics give similar but less obvious effects upon the vulva. Removal of the sacral spinal cord does not prevent their action.

Aberrant Course. Besides the two courses described above by which the lumbar spinal nerves send fibres to the external generative organs, there are various other possible courses.

In the first place, the aortic plexus sometimes gives off a filament to the pelvic plexus, and this may contain a few fibres for the generative organs. Thus if both hypogastric nerves are cut about an inch below the inferior mesenteric ganglia, and both sympathetic nerves cut just above the 7th lumbar ganglia, and then both sympathetics are stimulated from the 3rd to the 6th lumbar ganglia, a slight retraction of the penis is occasionally obtained; the retraction is no longer obtained after tearing away the aortic plexus. The fibres taking this course are undoubtedly homologous with the hypogastric fibres.

Secondly, a few fibres may leave the sympathetic at or below the 7th lumbar ganglia, and run in some other course than the pudic nerves. In order to determine this, we have had to make a considerable number of experiments.

At first, we exposed the branches of the pudic nerve from the ventral surface. Both sympathetics were stimulated just above the 7th lumbar ganglia, and the usual contraction noted. It was somewhat less than normal owing to the exposure of the parts during the dissection of pudic nerves. The pudic nerves were then cut on both sides, and the sympathetic again stimulated. In six such experiments on rabbits (one being female), we were unable to observe any effect from stimulation of the sympathetic after section of the pudic nerves.

We then exposed the pudic nerve from the dorsal surface. Since it

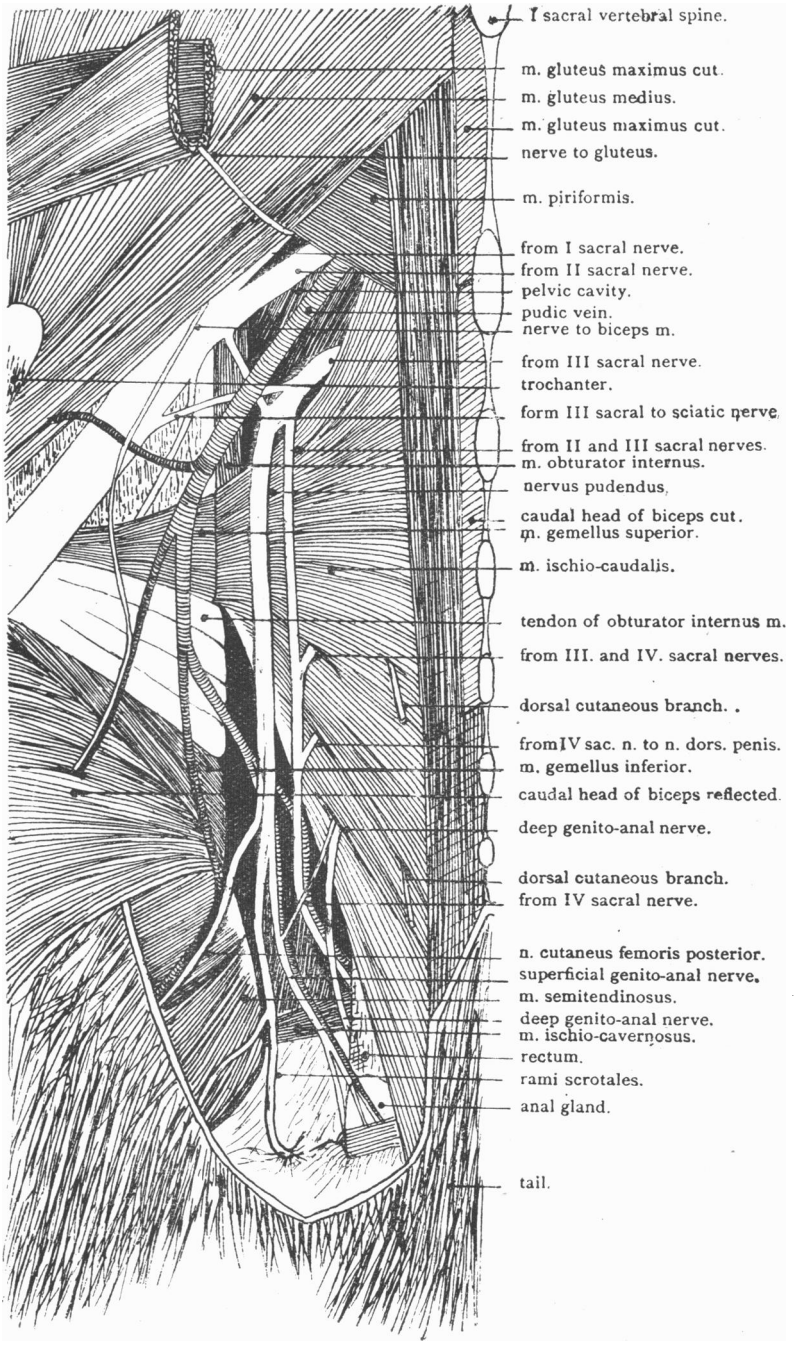

FIG. 3. Structures seen when the pudic nerve of the Rabbit is freely exposed from the dorsal surface. Twice the natural size. The nervus cutaneus femoris posterior, superficial genito-anal, and scrotal nerves, are represented for the sake of clearness as forming one trunk, in fact they are only loosely attached to one another. Posterior arrangement of nerves.

requires considerable experience to recognize readily the various origins and branches of the pudic nerve, when dissected without unnecessary exposure, we give below sketches of the surroundings of the pudic nerve in the rabbit and cat, when it is exposed in the greater part of its course from the dorsal surface.

In the rabbit, after section of the pudic nerves, the sympathetics at the level of the 7th lumbar ganglion gave no effect in three females and one male; but in one male, the sympathetics caused slight retraction and pallor of the penis, without any retraction of the genito-anal skin. In these experiments, the tissues were observed externally.

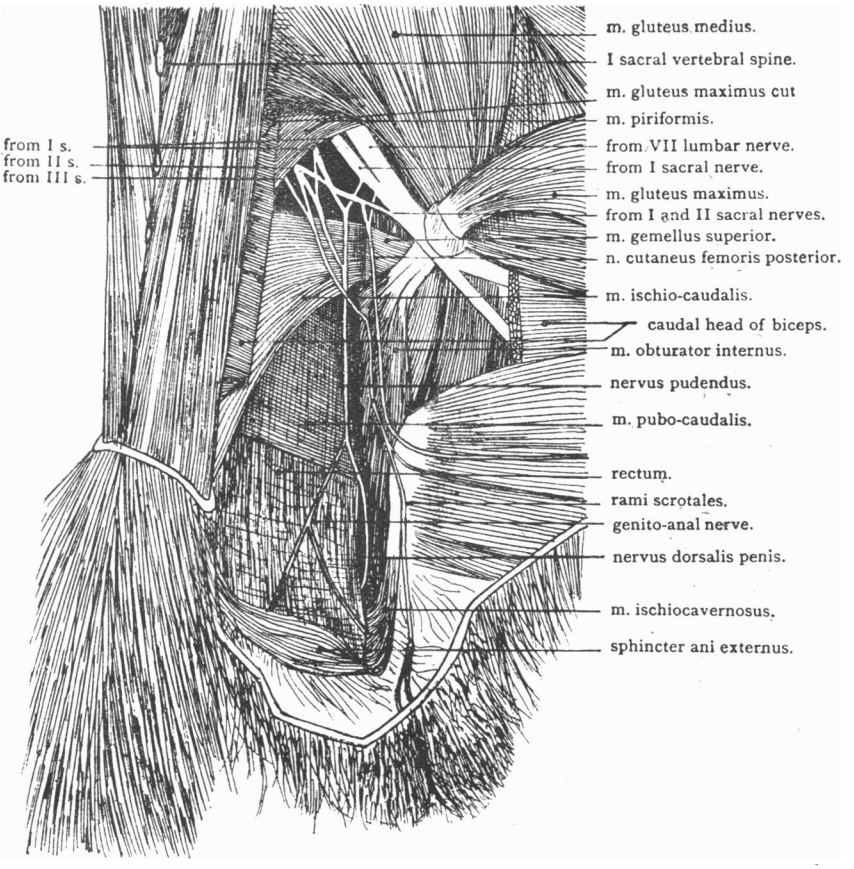

FIG. 4.

Structures seen when the pudic nerve of the cat is freely exposed from the dorsal surface. Natural size. Posterior arrangement of nerves.

Five experiments were made on cats, all being males. In three of these, the sympathetics had no effect after section of the pudic nerves. In the other two, the sympathetics caused slight retraction of the penis, provided the penis was in a state of considerable erection at the moment of the sympathetic stimulation.

Although we have only found the lower lumbar sympathetic to be effective, after the pudic nerves have been cut, in three out of fourteen cases; yet we think that usually a few nerve fibres for the penis (or clitoris) do run by way of the lower lumbar sympathetic chain without passing to the sacral nerves. The frequent failure to show them experimentally was we think due to insufficient attention to the conditions of success. We append a brief account of one of the successful experiments (cp. also Part II. p. 76).

Protocol III[1]. *Cat. Effect of stimulating the sympathetic below the 7th lumbar ganglion after section of the pudic nerves.* Chloroform, then A. C. E. by tracheal tube. Pudic nerves exposed dorsally on both sides. Cut through lower part of linea alba, double tie and cut femoral vessels. Tie and cut sympathetic trunk on each side, just below the 7th lumbar ganglion; isolate each up to the 1st sacral ganglion.

Stim. lower cut end of left sympathetic. Strong contraction of tunica dartos (both sides), strong retraction and good pallor of penis, strong erection of hairs of tail.

Stim. right sympathetic. Effects like those of left sympathetic.

Cut on both sides the exposed pudic nerves, not including the perineal branches.

Stim. left sympathetic. Strong contraction of tunica dartos, and erection of hairs, no effect on penis.

Stim. right sympathetic. Effect as on left side.

Cut on both sides the perineal nerve.

Stim. both sympathetics. No effect seen on penis, prepuce, scrotum or bladder. Strong erection hairs of tail.

Tie and cut both hypogastric nerves just below the inf. mesenteric ganglia.

Penis now projects, are some spontaneous variations in size; when a considerable excess of the A. C. E. mixture is given there is some shrinking of the penis.

Stim. left hypogastric. Good contraction of bladder, vas deferens, seminal vesicle, slow contraction of internal anal sphincter. No certain effect on the penis.

[1] Protocol I. in Part I. p. 78, and Prot. II. in Part II. p. 76.

Tie and cut medio-posterior branch of nervus erigens on the left side. Stimulate this branch of the nervus erigens to obtain projection of penis.

Stim. hypogastrics. Distinct retraction of penis.

Cover up for ten minutes. Penis again projected.

Stim. hypogastrics. Retraction of penis.

Stim. sympathetics. No certain effect on penis, strong erection of hairs of tail.

Stim. nervus erigens to obtain projection, then stim. sympathetics. Slight retraction.

Cover up for ten minutes. Penis projected.

Stim. sympathetics. Slight retraction.

Stim. hypogastrics. Slight further retraction.

The exact course taken by these fibres is not easy to determine. We do not think they run by the sacral grey rami to the spinal nerves and then peripherally in the nervus erigens, since such fibres should not be paralysed by nicotin (cp. Part V.) and after nicotin has been given, stimulation of the nervus erigens near its origin has no effect on the generative organs. Nikolski described in the dog a filament running from the 7th lumbar ganglion to that ramus of the nervus erigens which arises from the 1st sacral nerve. We have sometimes found such a filament running direct to the pelvic plexus near the entrance into it of this anterior ramus[1]. Some of the upper lumbar fibres run we think in this filament, or in a corresponding filament from the 1st sacral ganglion. These, like the fibres which branch off from the aortic plexus, we take to be homologous with hypogastric fibres. But as each sympathetic ganglion gives off some fibres to the neighbouring arteries, it is possible that a few lumbar fibres may run to the generative organs by way of the arteries supplying them, without traversing the pudic nerves, or the pelvic plexus.

But whatever the course may be, it must be borne in mind that the total number of fibres which take any other course than that of the pudic nerves or the hypogastric nerves is extremely small.

QUESTION OF INHIBITORY FIBRES IN THE HYPOGASTRIC NERVES.

We have already said that we have found no satisfactory evidence of the presence in the lumbar spinal nerves of vaso-dilator fibres for the generative organs. Repeated experiments on stimulation of the

[1] In one case (dog) a filament was given off by the 7th lumbar ganglion to the lower part of the hypogastric *nerve*.

nerves in the peripheral part of their course, namely, in the sympathetic trunk at the junction of the lumbar and sacral region, and in the hypogastric nerves, have not given us any indication of the existence of erector fibres in them. The absence of erector action on stimulating the hypogastric nerves was the more surprising, since Budge has described erector action from the hypogastrics in the rabbit, and François-Franck from the hypogastrics in the dog. Budge observed the action directly. It is not impossible that the erection observed by him should have been brought about reflexly (cp. Part I. p. 69), or by an escape of current to the sacral erector fibres in the pelvic plexus. François-Franck deduced the presence of erector fibres, from the curves obtained by the graphic method. The interpretation of the curves does not seem to us to be by any means a simple matter. It is hardly necessary to criticise them at present, for if the hypogastric nerves have any such dilator effect as is attributed to them by François-Franck, it must be visible to the eye, when the penis is exposed. In the rabbit and cat taken together, we have in more than thirty cases, and in the dog in seven cases, observed the external generative organs during stimulation of the hypogastric nerves. In the cat and rabbit, there was, as a rule, some degree of contraction. But we have not once seen dilation of the blood vessels or erection. On the lumbar sympathetic, our experiments have been more numerous and the results similar. Since slow rhythmic shocks are held by some to be more effective on vaso-dilator than on vaso-constrictor nerves, we have occasionally stimulated the lumbar spinal nerves and the hypogastrics with induction shocks repeated once a second, instead of with tetanising currents; constriction and not dilation was still obtained. When stimulating the sacral nerves—or the nervi erigentes—we have no difficulty in obtaining erector action. We think, then, that the evidence does not warrant the view that there are erector nerve fibres in the lumbar spinal nerves, or in the hypogastrics.

The lumbar nerves or the hypogastrics, though unable normally to cause micturition, often force a little urine into the upper part of the urethra. In such case the urethra may contract reflexly. And the reflex may affect other genital muscles, and cause some movements of the penis. Occasionally we have seen fairly strong contraction of the whole genito-anal striated muscles to be set up in this way. It is possible that similar contraction should be set up when the seminal vesicles force their contents into the urethra. Some movement of the penis may also be caused by the contraction of the muscles of the rectum.

The Lower set of Nerves.

Function in the Male. Some of the effects of the lower set of nerves are well known, namely:

(1) *Flushing and swelling of the penis.* With unilateral stimulation, the effect can usually be seen to begin on the stimulated side; thus in the rabbit, after curari, if the prepuce be held back, stimulation of the nerves on one side may cause the penis to project and curve towards the opposite side. A slight swelling of the organ easily escapes notice if its projection from the prepuce is alone looked for. In all doubtful cases, the prepuce should be cut through and the penis separated from the surrounding tissue as far as the limb muscles.

(2) *Contraction of the striated erector muscles,* viz. the recto-cavernosus, the ischio-cavernosus, the bulbo-cavernosus, Houston's muscle and the striated muscle of the urethra. In the rabbit there is also the pubo-cavernosus. In the cat, the bulbo-cavernosus on either side is prolonged along the ventro-lateral part of the penis, running on either side of the urethra, as far as the attachment of the prepuce. In the cat also, there is an elevator of the scrotum, which causes the scrotum to be drawn sharply towards the anus; this movement appears to aid considerably in the protrusion of the penis. Unilateral nerve stimulation causes the penis to be pulled forcibly towards the stimulated side. In the cat and rabbit, when the penis is freed up to the muscles of the limb, the upper set of nerves cause the penis to straighten with a jerk, and to shoot out a little (contraction of the bulbo-cavernosus). As a rule there is simultaneously a strong ejaculator urinæ action, a drop or two of urine being violently ejected. There is a similar spirt of blood, on stimulating the upper set of nerves after the penis has been cut through at the level of the attachment of the prepuce; this does not occur after curari has been given; it is clear that normally the contraction of the striated muscles must drive violently forward a few drops of blood into the anterior end of the penis.

Other effects are:

(3) *Inhibition of the retractor muscle.* This is most readily seen in the dog, and in the dog it is a very striking phenomenon. When the muscle is cut through at its insertion in the prepuce, and the connective tissue on either side is also cut through for 2 to 3 centimetres, stimulation of one of the effective lumbar nerves causes it to

contract and to be drawn more or less completely into the connective tissue sheath which covers it. When the cut end is lightly pulled with forceps, there is clearly felt resistance to extension, and it is one to two minutes before the (approximate) original length is obtained. When however the sacral nerves are stimulated immediately after the lumbar nerves, there is a period of 10 to 20 seconds, during which the resistance to extension is felt as in the first case, but then the muscle begins to yield, and it is, with very gentle tension, rapidly drawn out to full length. If the muscle is left untouched, it sometimes becomes obviously flaccid on stimulating the sacral nerves. It is not difficult in this manner to satisfy oneself of the presence of inhibitory sacral fibres, notwithstanding the movements caused by the simultaneous contraction of the genito-anal striated muscles. The effect of these can of course be abolished by curari. But in an experiment like that given above, some movement of the cut end of the retractor will be caused by certain of the unstriated muscles of the genito-anal apparatus apart from a direct action on the retractor. Thus, contraction of the recto-coccygeal muscle may press posteriorly the external anal sphincter and so allow the cut end of the retractor to move anteriorly (cp. Fig. 1, p. 89). The considerable swelling of the bulb of the penis has a tendency to force the cut end of the retractor backwards. The method by which the inhibition of the retractor muscle can be most conclusively shown is perhaps the following. In an anæsthetised dog, one of the effective lumbar nerves (say the 3rd) and the cauda equina are prepared for stimulation. Morphia and curari are then injected into a vein. The retractor muscle is cut at its insertion and tied by a thread, which is carried over a wheel to a weighted lever; the muscle is isolated as far as the posterior part of the bulb, here it is clamped with just sufficient firmness to prevent it sliding in the clamp, which can be done without stopping the passage of nervous impulses. The part of the muscle between the clamp and the tied end cannot be moved by the contraction of the rest of the muscle, or by any other muscle; it is practically isolated from the body except as regards its nerve-supply. Yet the relaxation on stimulating the cauda equina, is in favourable circumstances almost as obvious as the immediately preceding contraction on stimulating the lumbar nerve. On simultaneous stimulation of the lumbar and sacral nerves, so far as our scanty observations on this point go, the contractor effect overcomes the inhibitory, except when the stimulation of the lumbar nerve is very weak.

4. *Inhibition of the unstriated muscles of the genital skin.* Stimu-

lation of the lower set of nerves causes a movement of the skin—provided of course the fibres have some tone—in the opposite direction to that produced by the upper set of nerves (cp. Fig. 2). In the rabbit only, is the effect an obvious one; the skin which overlies the body of the penis moves posteriorly and ventrally, so that it and the lower end of the rectum become farther apart. The movement is to a considerable extent passive, due partly to the increase in the volume of the penis, and partly to the longitudinal contraction of the rectum, but it is partly due to inhibition of the skin muscles, since it may be seen when precautions are taken that other agencies shall have no effect. When curari is not given, the striated muscles at the base of the penis may counteract the inhibitory downward movement. In the cat, the lower set of nerves cause the prepuce and anus to move farther apart, but the movement is slight and whether it is due to inhibition of skin muscles we have not determined.

The sacral nerves have not, apparently, any inhibitory fibres for the unstriated muscle of the scrotum. In the rabbit the contraction caused by the lumbar nerves is so slight, that we could hardly expect a marked inhibitory effect from the sacral nerves. But in the cat, and still more in the dog, strong contraction is produced by the lumbar set of nerves, and nevertheless we have never been certain of any increase in the rate of relaxation on stimulating the separate sacral nerves or the cauda equina. Now and then we have thought there was a slight inhibition, but since in no experiment was the effect constant, or even frequent, we think it was simply the expression of normal variations in the relaxation rate.

Nor do we find that the sacral nerves contain vaso-dilator fibres for the scrotum; occasionally on stimulating these nerves in the rabbit there was slight flushing, but owing to its infrequency and inconstancy we think it was due to 'spontaneous' variations, and not to the stimulation of inhibitory sacral fibres.

All of the effects spoken of above are produced by nerve fibres which run from the spinal cord in the sacral nerve roots. Besides these, there may be seen, on stimulating the sacral nerves in the vertebral canal, other effects which, as we shall show later (p. 108), are not caused by nerve fibres issuing from the sacral spinal cord. The effects are, pallor and retraction of the penis, contraction of the prepuce and genital skin, contraction and pallor of the scrotum, in short, all the effects produced by the upper set of nerves. Thus on stimulating an

effective spinal nerve near its exit from the vertebral canal, there is commonly a struggle between two antagonistic actions; at times one, at times the other predominates, and a slight shifting of the electrodes may vary the degree or the nature of the predominance, hence the actual changes observed vary very widely. The contractor effects are more easily produced in the rabbit than in the cat, and more easily in the cat than in the dog.

Lastly we may notice an observation by V. Anrep and Cybulski[1]. They found in the dog that the nervus erigens caused normal swelling of the penis after intra-venous injection of 30 mgr. of atropin. We have injected up to 60 mgr. of atropin into the jugular of the rabbit, and find similarly that none of the actions of the sacral nerves on the external generative organs in male or female is appreciably affected.

Function in the Female. Here, as in the male, two groups of effects, antagonistic to one another, may be produced by stimulating the lower set of nerves in the vertebral canal, and as in the male, only the nerve fibres which have an inhibitory action run from the spinal cord in the sacral nerve roots. The inhibitory effects are: (1) Flushing of the mucous membrane of the vulva, and still more of the clitoris. (2) Dilation of the vulva. In the rabbit this is often very marked, it is greatest at the vulvar orifice and least immediately above the orifice; it is best seen when the vulva is held open in a state of slight tension. In the cat and dog, this effect is slight or absent. (3) Relaxation of the skin muscles around the vulva. In the rabbit, the whole surrounding skin moves ventrally, that over the end of the rectum moves dorsally; the movement corresponds with that we have described in the male.

The visceral motor effects are the same as those produced by the upper set of nerves (p. 94) and we need not repeat them.

Besides these effects there is of course contraction of what is usually called the external sphincter of the vagina and of the striated muscles which correspond with the striated genital muscles of the male. In the rabbit the external vaginal sphincter is situated towards the anterior portion of the vulva, and not near its opening. In the dog, on stimulation of the sacral nerves, the vulva is pulled dorsally so that the upper part disappears under a fold of skin.

[1] Hofmann and Schwalbe's *Jahresb.* 1884, p. 49.

Motor visceral effects of stimulating the sacral nerves in the spinal canal. The first point that demands attention is the motor visceral action (contraction of unstriated muscle fibres) given by the sacral nerves. It has been shown[1] that in certain cases the sympathetic fibres which run in a grey ramus to a spinal nerve can be stimulated by stimulating the spinal nerve in the vertebral canal. And we have shown above (p. 96) that the sacral sympathetic sends motor visceral fibres to the sacral nerves by way of the grey rami. There is then a certain likelihood that the contraction and pallor of the generative organs, which can be produced by stimulating the sacral nerves in the vertebral canal, are due to excitation of sympathetic nerve fibres. And this we find to be the case.

The obvious way of testing the matter is to stimulate the nerve roots as far as possible from the grey ramus, *i.e.* as near as possible to the spinal cord. When this is done, and proper precautions are taken to prevent the electric currents from spreading down the nerve, inhibition, *i.e.* erector action only is obtained. Some care, however, is required to obtain the nerve roots in the normal state of irritability so that weak shocks only need be used.

It is not absolutely necessary to take the nerve roots, for as a rule, weak stimulation of the nerves just peripherally of the posterior root ganglia gives inhibitory effects only; contractor effects begin to be seen as the electrodes are shifted still more peripherally; they are most marked when the nerves are stimulated at their point of exit from the bone, and stimulated with a strong current. In the cat, the erection of hairs in the local area of the nerve stimulated affords a useful indication that fibres of the sympathetic grey ramus of the nerve are being stimulated.

The question may be approached in another way. If the roots of the spinal nerves contain motor visceral fibres, they must run either in the pelvic visceral nerves or in the pudic nerves. But when the sacral nerves are stimulated, after section of the pudic nerves, inhibition and erection only are obtained; so that no motor fibres—or more strictly, no appreciable number of them—are contained in the pelvic visceral nerves (nervi erigentes) at their origin.

With regard to the other possible course of motor fibres, namely, the pudic nerves, we can compare the motor effect of any one branch with that of the sympathetic fibres which go to the branch. Thus suppose

[1] Langley. This *Journal*, xv. 203. 1893; xvii. 311. 1894.

in the cat all the branches of the pudic nerves are cut except the perineal branch on one side. If then the perineal nerve receives motor visceral fibres from the sacral nerve roots as well as from the sympathetic, it should be capable of producing with a weak stimulus a stronger contraction of the scrotum than that produced by a similar stimulus applied to the sympathetic trunk in the upper sacral region[1]. We do not find this to be the case.

Lastly we may note the action of nicotin on the sacral nerves. If the nerve roots contain motor visceral fibres for the external generative organs, they will—in accordance with the general law regarding visceral fibres—have nerve cells on their course, and the connections with the nerve cells will be paralysed by nicotin. In fact, when nicotin has been given, stimulation of sacral nerves in the vertebral canal still gives contraction and pallor in the generative organs and area, although it gives no trace of inhibitory or erector action.

We conclude then that the motor effects given by the sacral nerves are due to the stimulation of sympathetic fibres, and that the inhibitory effects only, are to be attributed to fibres issuing from the cord by the anterior nerve roots.

So far we have spoken broadly of the occurrence of motor visceral effects on stimulation of the sacral nerves. These effects are not however obtained with equal ease, nor with equal distinctness from each of the sacral nerves, nor are they necessarily obtained from all.

The ease with which the effects are obtained depends chiefly on the extent to which the fibres of the grey ramus can be stimulated by stimulating the spinal nerve in the vertebral canal. The longer the piece of nerve, which lies in the vertebral canal, the more easily and completely the grey ramus can be stimulated by stimulating the nerve. Thus the lower sacral nerves will give visceral motor effects, when stimulated a considerable distance from their point of exit, and with weak currents, whilst the 1st sacral in similar conditions gives little or no effect. The reason of this is that the grey rami of the lower sacral nerves penetrate the spinal canal in the nerve sheath before turning peripherally. The following diagrams will perhaps make the matter clearer.

A spinal nerve is shown passing out of an intervertebral foramen; *b* is the edge of the bones of the vertebræ; *p. pr. d.* is the posterior

[1] The argument of course would fail, if the sacral sympathetic sent any considerable number of fibres to the external generative organs by any other course than the pudics. (On this point cp. p. 98.)

primary division (dorsal division) of the nerve; *a. pr. d.* is its anterior primary division (ventral division); *symp. gang.* is the sympathetic ganglion; *gr. r.* is its grey ramus.

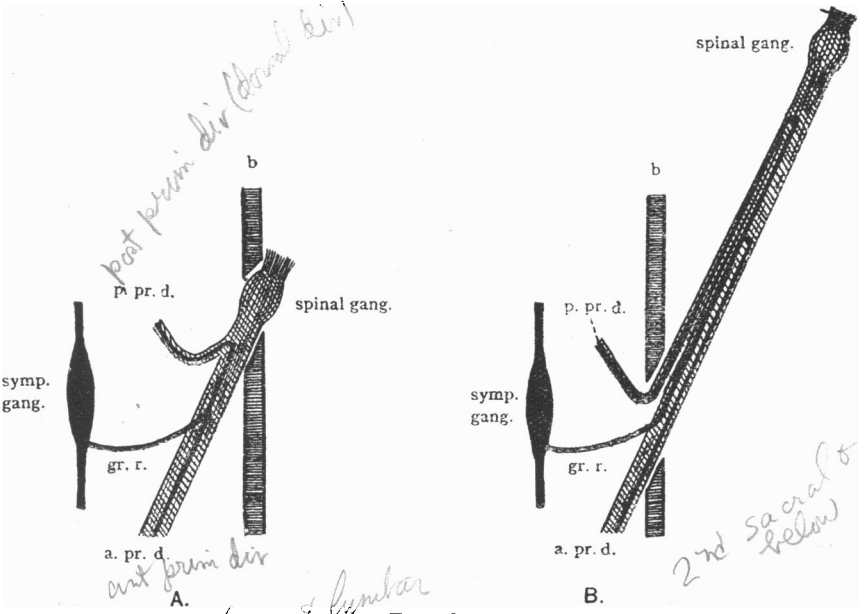

FIG. 5[1].

Fig. 5 A. is a diagram of the arrangement in the cervical, thoracic and lumbar regions. Here the grey ramus is outside the spinal canal and it will not be affected by moderate stimulation of the nerve roots inside the canal. When however the nerve is pulled into the spinal canal, and it is stimulated peripherally of its ganglion, there will be an escape current to the fibres of the grey ramus which run to the dorsal division of the nerve (*p. pr. d.*), and possibly also to those which run to the ventral division[2].

Fig. 5 B. is a diagram of the arrangement in the 2nd sacral nerve and of the nerves below it. Here the grey ramus can be stimulated in the spinal canal, and as the electrodes are passed down the nerve, the fibres to the dorsal division will first be stimulated, and then the fibres to the ventral division.

[1] Since the Figure is simply a diagram to show a special point, the fibres which run from the grey ramus to the dura mater are not inserted.

[2] Cf. Langley. This *Journal*, xv. 203. 1893; xvii. 306. 1894.

In the cat retraction and pallor of the penis and contraction of the scrotum can always be obtained by stimulating the 2nd sacral nerve near its exit from the sacral canal (cp. Exp. p. 114). The 3rd sacral nerve gives a moderate effect, when the arrangement of the nerves is posterior. The 1st sacral nerve gives little or no viscero-motor effect, unless a strong current is used, and then it is but slight, unless there is escape of current to the 2nd sacral nerve. If, however, the 1st sacral nerve is isolated nearly up to the sacral plexus, and the part which lies just outside the sacral foramen be stimulated, contraction of the penis and scrotum is readily obtained. We give an account of an experiment to illustrate this and some other points.

Protocol IV. *Cat (No. 62). Effects of stimulating the sacral nerves inside and outside the vertebral canal.* Nerves, median arrangement. Chloroform, later A.C.E. mixture. Expose sacral plexus on left side (cutting through ilium and edge of sacrum) so that the nerves are seen at their exit. Expose lower part of spinal cord, cut it through in mid-region of VIIth lumbar vertebra. Tie and cut on each side VIIth lumbar, I, II, III sacral and I coccygeal nerves a little above the posterior root ganglia, isolate them to their point of exit. Cut away bone at exit of I and II sacral, on the left side, and isolate them for half to three-quarters of a centimetre outside the sacrum. Stimulate the nerves with a tetanising current, secondary coil at 9 cm. of scale; shocks are distinctly felt on tip of tongue. The nerves on the right and left side were first stimulated near the posterior root ganglia. The results were:

VII Lumbar. Strong contraction of leg, toes widely separated, claws out. No effect on external sphincter, anus, or penis.

I Sacral. Strong contraction of leg, foot extended, toes bent a little backwards. Strong contraction of external anal sphincter and of elevator of scrotum. Moderate protrusion of penis, some flushing.

II Sacral. Toes bent. Moderate contraction of external anal sphincter, slight of elevator of scrotum. Penis a little protruded, some flushing. Contraction of ejaculator urinæ. Micturition after end of stimulation.

III Sacral. Strong micturition.

I Coccygeal. Tail movement only.

Cut through skin over penis in mid-ventral line to observe body of penis. Swelling of the penis is obtained from the Ist and IInd sacral nerves. The IIIrd sacral nerves (the two stimulated together) cause apparently a slight swelling, but the result is too inconstant to be quite certain about.

Separate body of penis from surrounding connective tissue and stimulate on left side Ist and IInd sacral nerves a little outside the sacral foramina.

I Sacral. At once, some protrusion and straightening of penis from contraction of its striated muscles (including ejaculator urinæ), then great retraction, shrinking, and flaccidity.

II Sacral. Rather less protrusion and straightening of penis, otherwise effects like those of the Ist sacral.

Cut on left side the filament sent by IIIrd sacral nerve to the nervus erigens. Stimulate the IIIrd sacral near its exit. There is apparently some retraction of the penis, but it is not sufficiently constant to be certain about.

Cut through the linea alba and observe the bladder, stimulating the sacral nerves on both sides.

I Sacral. No effect from either nerve.

II Sacral. Good contraction from both nerves.

III Sacral. Good contraction from right nerve, none from left (cp. above, strand to nervus erigens cut).

I Coccygeal. No effect from either nerve.

In the rabbit, the 4th sacral nerve, stimulated in the spinal canal near its exit, always gives strong viscero-motor effects; with an anterior arrangement of nerves, the 3rd sacral gives a moderate, and the 2nd sacral (usually) a slight effect; with a posterior arrangement of nerves, the 3rd sacral and the 1st coccygeal nerves give a moderate effect.

From the results of experiments on stimulation of the spinal nerves inside and outside the vertebral canal, and on stimulating the sacral ganglia or grey rami, we come to the following scheme as to the grey rami which supply the external generative organs, and as to their relative degree of action. We must state, that we have not made a sufficient number of experiments to be quite certain of all the points of this scheme; the doubtful points we have queried.

	Cat			Rabbit	
	Anterior	Median	Posterior	Anterior	Posterior
VII L.	0	0	0	0	0
I S.	G	G	?M	?S	0
II S.	G	G	G	M	?S
III S.	?0	0 or S	S M	G	G
IV	0	0	0	M	G
V	0	0	0	0	S M

It will be convenient to give here the several effects which we have observed on stimulation of the various branches of the pudic nerve in the male. In the female, corresponding results are obtained.

Rabbit. The *superficial genito-anal* causes strong contraction of the external sphincter of the anus and vagina, of the recto-cavernosus, the ischio-cavernosus and bulbo-cavernosus, and some contraction of the urethra. The only visceral effect it produces is a contraction in the posterior part of the skin over the rectum, and this is due to a filament it receives from the deep genito-anal. When the branches of the nerve are taken, good contraction of the external sphincter can be obtained from several of them.

The *nervus dorsalis* causes strong contraction of the pubo-cavernosus, of Houston's muscle and of the urethra. Its visceral effects are strong contraction of the intrinsic muscles of the penis, of the blood vessels of the penis; strong contraction of the prepuce, moderate contraction of the rest of the genital, but not of the anal skin.

The *deep genito-anal* causes some contraction of the bulbo-cavernosus and of the urethra near the bulb. Its visceral effects are contraction of skin muscles both of the anal and genital skin (cp. Fig. 2).

The *perineal nerve* causes slight contraction of the tunica dartos and of the blood vessels of the scrotum.

Cat. The *nervus dorsalis* has a similar action of that in the rabbit except that it has less effect upon the body of the penis.

The *genito-anal nerve* has the combined action of the superficial and deep genito-anal in the rabbit, and in addition causes contraction of the body of the penis.

The *scrotal nerves* cause strong contraction of the tunica dartos of the scrotum on the same side.

Origin of the nerve fibres for the genital striated muscle.

Cat. The external sphincter of the vagina is, so far as we have observed, supplied with motor fibres by the same nerves as supply the external sphincter of the anus. This was the case in Exps. 6, 2, 5, 45, 13, 28, 26, 29 (cp. Part I. p. 95). Broadly speaking the same holds for the striated muscles of the penis. It was the case in Exps. 1, 32, 40, 4, 50 (cp. Part I. p. 95). The correspondence in the origin of the motor fibres for the external anal sphincter and for the striated genital muscles has obtained also in later experiments. The only one we need quote is that given below in which the nerves were markedly anterior, and the 2nd sacral nerve instead of causing strong contraction of the external sphincter of the anus and the muscles of the penis had a very slight effect.

Protocol V. *Cat* (*No.* 59). *Effects of stimulation of sacral nerves. Nerves markedly anterior.* Chloroform, later A. C. E. mixture. Expose spinal

cord from the 7th lumbar vertebra downwards; cut it at the upper level of the vertebra. Tie on each side a little centrally of the posterior root ganglion the VIIth lumbar, I, II, III sacral and I, II coccygeal nerves. Isolate them up to their points of exit. Small pieces of sponge were placed in the canal between each pair of nerves, these were removed on both sides of a nerve before stimulating it. For stimulation, a tetanising current was used; the shocks were distinctly felt on the tip of the tongue, but not strongly, with the secondary coil at 10 cm. of scale (= c. at 10). Stimulate the nerves in succession close to the ligature; c. at 10; the nerve on each side was stimulated several times. The results were:

VII Lumbar. Strong contraction of leg, toes wide apart, and claws out. If the electrodes are allowed to touch the cut edge of the bone, or even if passed down the nerve close to its exit, there is also contraction of the sphincter of the anus; but with careful isolation, the nerve being stimulated near the ligature, there is no effect on the external anal sphincter, or on any of the genital muscles.

I Sacral. Strong contraction of leg and foot, but toes not separated nor claws put out. Very strong contraction of external anal sphincter. The scrotum is forcibly drawn up towards the anus. Strong protrusion of the penis, which becomes more flushed at tip. Prepuce is drawn back.

II Sacral. Toes bent. Slight to moderate contraction of external anal sphincter with the left nerve, very slight with the right nerve. Scrotum not drawn up. Penis not protruded, but is seen to swell when prepuce is held back. Micturition, sometimes after, sometimes during stimulation. Some defæcation.

III Sacral. Movement of tail. No effect on external anal sphincter, elevator of scrotum or muscles of penis, and no certain effect (prepuce being held back) on penis itself. Some micturition with earlier stimulations.

I Coccygeal. No effect, except movement of tail.

Use now a stronger current (c. = 8) and stimulate the nerves near their *exit from the bone.* The prepuce was held back by small clamps. The results were (omitting muscular effects described above):

I Coccygeal. } No effect seen in penis or tunica dartos of scrotum. Good
III Sacral. } erection of hair in the region supplied by the nerve stimulated.

II Sacral. Good retraction of penis; and contraction of tunica dartos on the stimulated side.

I Sacral. Sometimes slight contraction of tunica dartos.

The prepuce was cut through, and the body of the penis freed from the surrounding tissue. (c. = 9).

VII Lumbar. No effect on penis.

I Sacral. (Before 1st stimulation, penis retracted.) Strong contraction of ejaculator urinæ; penis swells gradually but greatly, and remains so. On stimulating again, there is quick strong extension and straightening of penis.

II Sacral. Penis quick movement, extends and becomes straighter, movement is slight compared with that produced by I sacral, penis swells; when the electrodes are moved towards the exit of the nerves, there is retraction and curving of the penis.

Expose spinal cord in lower lumbar region. Tie and cut on each side IV, V, VI lumbar nerves. Remove the cord in this region. I Sacral, erection; then stimulate IV lumbar, the penis contracts, is bent dorsally by the retractor muscle, then shrinks further and becomes flaccid; II Sacral, erection, then stimulate Vth lumbar, no effect; then IVth lumbar, there is very strong retraction of penis; stimulate III sacral, no effect seen, and no effect with VIth or VIIth lumbar.

Cut through abdominal wall in linea alba to expose the bladder. Inject into jugular vein 2 c.c. 1 p.c. curari, in order to paralyse the striated genital muscles.

I Sacral. Slight to moderate contraction of bladder, strong swelling of penis.

IV Lumbar. Slight to moderate contraction of bladder, great shrinking of penis, contraction of vas deferens and of tunica dartos of scrotum.

II Sacral. Strong contraction of bladder, strong swelling of penis.

III Sacral. Fairly strong contraction of bladder; no certain effect on penis.

V Lumbar. No effect on bladder or penis.

Inject into jugular, 25 mgs. nicotin. After this no nerve caused contraction of the bladder or swelling of the penis. The IInd sacral nerve stimulated near its exit caused retraction of the penis and contraction of the tunica dartos.

The scheme of innervation of the striated genital muscles of the cat, both male and female, is then

	Markedly Anterior		Moderately Anterior, Median and Posterior (*a*)	Posterior (*b*)
	i	ii		
VII	0	0	0	0
I	**G**	**G**	**G**. G[1]	G
II	S	M	G	**G**
III	0	0	0	0

[1] In some instances of Median and Posterior (*a*) Class, we have not noticed that the 1st sacral gave a stronger effect than the 2nd sacral nerve, but we have not worked the matter out.

So far as regards the nerves which are effective, our results agree with those of Sherrington on the external sphincter of the vagina. Sherrington treats somewhat broadly the variations in origin which correspond with variations in the arrangement of the nerves. He states that in his experiments the 2nd sacral gave usually a greater effect than the 1st, on the vaginal sphincter, *i.e.* presumably in the whole post-fixed class. In the summary of the characteristics of the pre-fixed class (*op. cit.* p. 640) he gives the 2nd sacral as having a slight effect only. Both of these appear to us to be extreme variations, of the former we have observed one instance only, and of the latter but two.

The several striated muscles of the genito-anal region are not, however, innervated in exactly the same way. If they were the complex movement produced by the 2nd sacral nerve should be the same as that produced by the 1st sacral, except in strength. But this is rarely, if ever, the case. In all cases, when we have noticed carefully the character of the movements produced by the two nerves, there were some differences. Thus when the penis is freed from surrounding tissue up to the limb-muscles, the 1st sacral may cause chiefly a ventral movement of the penis, whilst the 2nd sacral may cause chiefly an outward, straightening movement. Nevertheless, the only muscle which we have definitely found to be innervated by a single spinal nerve is the elevator of the scrotum. And this only when the arrangement of the nerves is markedly anterior (cp. Exp. above).

In the rabbit, also, we have found no certain difference[1] between the origin of the nerves for the striated genital muscles and that of the nerves for the external anal sphincter. A correspondence in their origin was observed in the experiments given in Part I. p. 92. In male animals the protrusion of the penis, in female animals the contraction of the external vaginal sphincter, was observed at the same time as the contraction of the external sphincter of the anus. Since writing Part I. we have made further experiments, and with similar results. One of these we may mention, since the arrangement of nerves was more posterior than any we had met with previously. In this (No. 34), the 2nd sacral nerve gave a slight contraction only, the 3rd and the 4th sacral both gave a strong contraction.

Taking all our experiments into consideration, we deduce the

[1] In Exp. No. 28, in which the 4th sacral nerve caused slight contraction of the external sphincter, it did not cause any jerking movement of the penis, but as the genital muscles were not exposed they may have contracted slightly.

following scheme for the innervation in the rabbit of the striated muscles of the external generative organs.

	Anterior	Median to Posterior	Posterior (α)	Posterior (β)
I	0	0	0	0
II	G	G	G	S
III	G	G	G	G
IV	0	0	S	G
I	0	0	0	0

It will be noticed that there is greater variation in the innervation of the somatic genital muscles in the rabbit than there is in the cat.

In the rabbit as in the cat, the movement of the penis produced by the several nerves varies somewhat in character, and we think it possible that, in both, particular muscles are innervated by a single nerve.

Origin of visceral erector fibres.

On the origin of the inhibitory fibres to the external generative organs, we have made a large number of experiments. The results were the same in the male and the female, so that we may treat these together. Most of the experiments were made by stimulating with weak and with strong tetanising currents the several sacral nerves, and observing the various results produced. One point especially must be noticed. The degree of protrusion of the penis caused by a particular spinal nerve is no satisfactory indication of the number of vaso-dilator fibres it contains. Protrusion of the penis may be produced by the action of the striated muscles, independently of any coincident action of vaso-dilator fibres. All that is necessary for this, is that the penis be moderately distended with blood. Considerable and even great distension may be produced by section of the lumbar sympathetics. In such case great protrusion may be obtained by stimulating the pudic nerves which contain no dilator but only constrictor fibres. The protrusion, of course, is transient, the vaso-constrictor and retractor fibres soon coming into action. In the case however of the spinal nerves, the protrusion may continue, provided the stimulus be applied to the nerve in such a way as to avoid stimulation of the sympathetic fibres. For convenience the protrusion of the penis caused by the action of its striated muscles may be spoken of as somatic erection, and the enlargement of the penis produced by inhibitory fibres as visceral erection.

In both rabbit and cat, the lowest effective nerve nearly always produces pure visceral erection. With a markedly posterior arrangement of nerves, the highest effective nerve has once or twice appeared to produce pure somatic erection, but we have not been certain of entire absence of visceral effects.

The effect of the striated muscles can of course be done away with by giving curari. But on stimulating the spinal nerve in the most convenient place, *i.e.* peripherally of the ganglion of the posterior root, there still remains in most cases the conflicting action of the proper inhibitory fibres of the nerve and the motor fibres of the grey ramus joining it. With care the nerves which contain inhibitory fibres can nevertheless be determined, but it is certainly more satisfactory to cut the pudic nerves on one side at least before testing the spinal nerves for inhibitory fibres. Since, however, section of the pudic nerves, by cutting off constrictor impulses, may cause considerable distension of the penis, it may be advisable to stimulate the peripheral end of one of the pudic nerves in order to obtain constriction, and then to observe the effect of stimulating the spinal nerve.

The results we have come to regarding the origin of the inhibitory fibres, deduced from six experiments in which the pudics were cut and in about forty in which they were uncut, are as follows:

	Cat			Rabbit		
	Anterior	Median	Posterior (*a*)	Anterior	Median	Posterior
VII	0	0	0	0	0	0
I	G	G	M	0	0	0
II	G	G	G	G	S	?S
III	?0	S	S.M	G	G	G
IV	0	0	0	S	S.M	G
V	0	0	0	0	0	?0

In one or two experiments made on the dog, the origin of the inhibitory nerve fibres was the same as in the cat.

All the inhibitory effects of the sacral nerves are produced by fibres which pass out in the pelvic visceral branches (nervi erigentes). For (1) stimulation of the peripheral end of the cut pelvic nerves causes all the inhibitory effects we have mentioned above; and (2) if the nervi erigentes be cut, stimulation of the sacral nerves no longer has any inhibitory effect. The effects, if there are any, are motor.

Summary.

The upper—or lumbar—set of nerves cause, in the male cat, strong contraction of the arteries of the penis, slight contraction of the arteries of the surrounding genital skin and of the scrotum, strong contraction of the retractor muscle, and of the other unstriated muscle of the penis. These effects combine to produce considerable retraction of the organ. The nerves cause also strong contraction of the tunica dartos of the scrotum, and of the unstriated muscles of the prepuce; and contraction leading to slight movement in the surrounding skin.

In the male rabbit, the effects are the same except that there is very slight contraction in the scrotal skin, and there is marked contraction in the skin over the body of the penis.

In the dog, the effects are as in the cat, except that externally very little effect is seen. But the retractor muscle is readily exposed and its contraction is then conspicuous.

In the female, the effects are, *mutatis mutandis*, the same as in the male. But as a rule, they are less marked, and this is especially the case in the cat and dog with regard to the effects which are not vascular. In the rabbit, the movement of the skin covering the vulva is the strongest and most constant effect.

The origin of the nerves from the spinal cord, we take to be the same in the male and female, although the nerves which have a weak effect in the male, not infrequently have no perceptible effect in the female.

In the *cat*, the 13th thoracic and the 1st lumbar nerves sometimes send a few fibres to the genital arteries, causing slight pallor and shrinking, but we have not been certain of any other effect from these nerves.

The 2nd lumbar has as a rule a slight but quite distinct action on the external generative organs.

With an anterior arrangement of nerves, the 3rd and 4th lumbar have a strong action, and the 5th lumbar no action.

With a posterior arrangement of nerves, the 3rd lumbar has a slight to moderate action, and the 4th and 5th lumbar a strong effect.

In some cases, the nerves which cause contraction of the scrotum are as a whole anterior to those which have a distinct effect on the penis.

We have not worked out in detail the variations in the effect of the several nerves which may correspond with the variations in the forms of

the lumbo-sacral plexus, but judging from the experiments in which we have paid most attention to the matter they are as follows:

	Anterior	Median	Posterior (*a*)	Posterior (*b*)
II L.	S	S	?S	?S or 0
III L.	G	G	M	S. M
IV L.	G	G	G	G
V L.	0	0 or S	M	G
VI L.	0	0	0	0

In the *dog*, the innervation differs in two or three respects from that in the cat. The 5th lumbar does not send fibres to the external generative organs, even with a posterior arrangement of nerves; nor the 4th lumbar with an anterior arrangement. The 1st lumbar has a distinct action, and the same is the case with the 13th thoracic, and even with the 12th thoracic. The nerve fibres to the scrotum are more limited in origin than those to the penis; they arise from the 1st to the 3rd, or from the 2nd to the 4th lumbar nerves.

In the *rabbit*, we have found no effect from the 1st lumbar nerve (three) experiments, and twice only from the 2nd.

The 3rd, 4th and 5th lumbar nerves have always an effect, more or less pronounced.

The fibres from the lumbar nerves run in the white rami communicantes, to the sympathetic chain. From this there are two paths, the one (*a*) by the pudic nerves, the other (*b*) by the pelvic plexus.

(*a*) The great majority of the fibres take the course of the pudic nerves. They run down the sympathetic chain to the sacral ganglia. From these ganglia, fibres are given off, which run in the grey rami communicantes to the sacral nerves. The fibres run on in the pudic nerves (*i.e.* in somatic branches); sending, apparently, none to the nervi erigentes (*i.e.* to the visceral branches). The several sacral nerves take a different share in the formation of the pudic nerves in different individuals; and the effect which the several grey rami have on the generative organs varies in correspondence. The scheme of these variations is given on p. 112.

The pudic nerves vary only in origin, their peripheral distribution is the same in all animals of one species. The effects of stimulating the several peripheral branches is given on p. 113. This shows also the branches by which the sacral grey rami, *i.e.* the fibres from the lumbar nerves, make their way to the periphery.

(*b*) The second course, viz. that by the pelvic plexus, has compara-

tively few fibres. Most of them run in the hypogastric nerves. A few may join the plexus from the lower lumbar or upper sacral sympathetic chain, or from the aortic plexus. And of these some may join the first root of the nervus erigens, and run with it to the pelvic plexus.

The cremaster is absent in the rabbit and cat. It is present in the dog. Its motor fibres reach it by the genital branch of the genito-crural nerve, they arise from the 3rd or 4th lumbar nerves according as the plexus is anterior or posterior.

In the upper set of nerves we have found no satisfactory evidence of the presence of vaso-dilator fibres for the blood vessels, nor of inhibitory fibres for any unstriated muscle of the genital organs or genital skin.

The lower or sacral set of nerves cause, as is well known, contraction of certain striated genital muscles, dilation of the arteries of the penis (or vulva). They cause also inhibition of the unstriated muscle or body of the penis, the retractor muscle of the penis, of the vulvar muscles. The retractor muscle appears to us to offer advantages for the study of inhibition of unstriated muscular tissue, presented by no other muscle in which inhibition is known to occur. The sacral nerves cause also in the rabbit inhibition of the unstriated muscles of the genito-anal region.

The scheme of innervation of the striated muscles is given on pp. 115 and 117. That for the visceral inhibitory fibres on p. 118. The sacral nerves—so far as we have been able to determine—send no visceral fibres by their somatic branches.

When we compare the origin from the spinal cord of the nerves for the external generative organs with that of the nerves for the end of the intestine and for the bladder, we see that there is no essential difference as regards the lumbar nerves. The difference consists in the nerves near the junction of the thoracic and lumbar regions sending efferent fibres to the external generative organs more frequently than they do to the end of the intestine, just as these nerves more frequently send fibres to the end of the intestine than they do to the bladder.

With the sacral nerves however the matter is different. The origin of the inhibitory nerves which run to the external generative organs is more anterior than the origin of the nerves which run to the end of the intestine and to the bladder; the areas of origin overlap to a large extent, but the one extends a little farther towards the head, and the other a little farther towards the tail.

PART IV. THE INTERNAL GENERATIVE ORGANS.

By the internal generative organs we mean those which are not developed from the uro-genital sinus or from the surrounding skin. But to some of these we have paid very little attention. Thus, we have examined the testis and ovary in a few cases only, and then solely for vascular changes. The special parts observed, we shall mention below in the account of the results obtained in each animal.

Previous Observations[1]. The experiments of Valentin, Brachet, Longet, Budge, and others showed that contraction of the uterus could be obtained by stimulating the spinal cord—especially in the upper lumbar region—and by stimulating certain parts of the sympathetic system. Budge obtained contraction of the vasa deferentia in the rabbit by stimulating the spinal cord at the level of the 4th lumbar vertebra, and also by stimulating a certain sympathetic ganglion,—apparently the inferior mesenteric ganglion. Later Loeb obtained contraction of the vasa deferentia and prostate vesicles from the hypogastric nerves. Frankenhaüser, Körner and others found that

[1] Some account of the observations made before 1852 is given by Röhrig (quoted below). Compare also S. Meyer, Hermann's *Handbuch d. Physiol.* Bd. v. Th. 2. L. 1, p. 467. 1881.

Kilian. *Zeitsch. f. rat. Med.* N. F. II. 1. 1852.
Budge. *Virchow's Archiv*, XV. 115. 1858.
Spiegelberg. *Zeitsch. f. rat. Med.* R. III. Bd. II. 1. 1858.
Frankenhäuser. *Jenaische Zeitsch. f. Med.* I. 35. 1864.
Oberneier. *Experim. Unters. ü. d. Nerven des Uterus.* (Diss. Bonn.) 1865.
Körner. *Studien d. physiol. Instituts zu Breslau.* Hf. 3. 1865.
Loeb. *Beiträge zur Bewegung d. Sammleiter.* (Diss. Giessen.) 1866.
Frankenhäuser. *Die Nerven der Gebärmutter.* (Jena), 1867.
Oser u. Schlesinger. *Wiener med. Jahrbücher.* 1872. p. 57.
Schlesinger. *Wiener med. Jahrbücher.* 1873. p. 1.
Goltz u. Freusberg. *Pflüger's Archiv*, IX. 552. 1874.
v. Basch u. Hofmann. *Wiener med. Jahrbücher.* p. 465. 1877.
Röhrig. *Virchow's Archiv*, Bd. 76. p. 1. 1879.
Fellner. *Centralb. f. d. med. Wissensch.* p. 258. 1887.
Langley. *Proc. Physiol. Soc.* Dec. 1890. (This *Journal*, XII.)
Sherrington. This *Journal*, XIII. 684. 1892.

efferent fibres left the lumbar region of the spinal cord, and passed to the uterus by way of the sympathetic, the inferior mesenteric ganglia, and the aortic plexus. As to the origin of these fibres from the spinal cord, Langley found that most of them, both from the uterus and vasa deferentia, traversed the sympathetic in the region from the 4th to the 6th lumbar ganglion, so that presumably most of them arose from the 3rd, 4th and 5th lumbar nerves. Sherrington found that the 2nd and 3rd lumbar nerves in Rhesus, and the 3rd and 4th lumbar nerves in the cat, contained motor fibres for the vasa deferentia.

There is much difference of opinion with regard to the effect of the sacral nerves on the uterus. Frankenhaüser at first considered them to have an inhibitory action, later (1867) he withdrew this opinion and left the question open. Kehrer, Körner, and Röhrig state that they obtained contraction of the uterus on stimulation of the sacral nerves. v. Basch and Hofmann, and Fellner hold that the nervus erigens causes contraction of the longitudinal and inhibition of the circular coat of the uterus, and that the hypogastric nerve causes contraction of the circular and inhibition of its longitudinal coat. v. Basch and Hofmann also state that the nervus erigens contains dilator fibres, and the hypogastric nerve constrictor fibres for the uterine blood vessels.

Effects of the Upper Set of Nerves in the Female.

Rabbit. In the rabbit, the parts observed in all cases have been the uterus and the vagina. We made one or two experiments on the Fallopian tubes, they behaved exactly like the uterus. It will be remembered that in the rabbit the vestibule is well developed and is covered by a venous plexus which, when filled, forms an almost continuous and thickish layer of blood over it. The vagina stretches above this for six or more centimetres. It is of a rather opaque white colour, and has no venous sinuses. Its circular muscular coat is thicker than its longitudinal. It has sometimes been called the body of the uterus. There are two uteri joined by tissue for about three-quarters of a centimetre before they open into the vagina; this they do separately. They are sometimes called the cornua of the uterus.

The lumbar nerves have two effects on the uterus and on the vagina; they cause contraction of the small arteries, leading to pallor of the organ, and contraction of the whole musculature. The paling may take place very slowly, but the final state of pallor is nearly always great. The contraction of the muscular coats is as a rule very

strong; in the vagina the contraction can usually be seen to start from one end, and spread to the other; the whole then remains for a time in a state of powerful tonic contraction. The pallor and contraction do not commonly run a parallel course, sometimes pallor is obtained before contraction, and in rare instances there is pallor only. The uterus and the vagina do not always respond equally to nerve stimulation; and in such case either one or the other may be the more sluggish.

Cat. In the cat, the effects are of the same nature as in the rabbit, but they are in most cases less marked. Pallor is constant, but of very varying intensity. Contraction is inconstant, when it occurs, it is occasionally strong, usually it is weak.

Both in the rabbit and cat the contraction of the longitudinal muscular coat, on stimulating the lumbar nerve fibres in any part of their course, can be seen with the eye without difficulty. In favourable cases, the longitudinal shortening is most striking.

The lumbar nerves cause also contraction of the unstriated muscle fibres of the mesometrium, whatever their direction.

Stimulation of the lumbar nerves on one side causes at times slight contraction and pallor of the uterus on the opposite side.

The uterus and vagina become fatigued on frequent stimulation, sooner than any other of the organs we have dealt with; hence the longer the stimulus is applied, the longer should be the interval between the stimulations. Röhrig noted that atropin does not in the rabbit paralyse the motor fibres for the uterus. The maximum amount of atropin given by him is not stated. We have injected up to 50 mgs. into a vein, and so far can confirm his result. And similarly, after this amount of atropin strong contraction of the vasa deferentia and seminal vesicles can still be obtained by stimulating the peripheral ends of the hypogastric nerves.

Effects of the Upper Set of Nerves in the Male.

In the rabbit and cat we have in all cases observed the vasa deferentia, and in nearly all cases the seminal vesicles. The organs which in the rabbit we call for convenience seminal vesicles—as others have done on physiological grounds—are in fact the two-horned uterus masculinus. The uterus masculinus has been called also, for example, by Krause, the prostatic vesicle.

The lumbar nerves cause in both rabbit and cat, strong contraction of the whole musculature of the vasa deferentia and seminal vesicles. Pallor is also caused, but on account of the strong contraction, it is less evident as an independent phenomenon than the pallor of the uterus in the female.

The vas deferens in contracting becomes one to three centimetres shorter; so that here there can be no doubt that the longitudinal coat takes part in the contraction.

The contraction of the seminal vesicles is strong enough to cause emission of semen from the penis; we have mentioned earlier that the contraction of the bladder, which is caused by the lumbar nerves, is not strong enough to cause micturition.

Unilateral stimulation causes unilateral contraction of the vas deferens, and bilateral contraction of the seminal vesicles, beginning on the stimulated side.

In the dog, the contraction of the vas deferens, on stimulation of the upper lumbar nerves, is as a rule not very obvious, and there is little or no longitudinal contraction. In sections of the vas deferens it is seen that the musculature is arranged almost entirely in a circular manner. Thus it appears that in the cat and rabbit the shortening of the vas deferens is brought about by the contraction of its intrinsic unstriated muscle, whilst in the dog, this is effected in its upper (testicular) region only and by the action of the striated cremaster muscle (cp. Part III. p. 92).

Origin from the Spinal Cord of the Lumbar Nerve Fibres.

In the rabbit, we have not noticed that any effect is produced on the uterus, the vagina, the vasa deferentia or seminal vesicles, by stimulating the sympathetic chain above the 3rd lumbar sympathetic ganglia. The sympathetic between the 3rd and the 4th lumbar ganglia usually gives slight contraction and pallor, but sometimes there is no effect. Between the 4th and the 6th lumbar sympathetic ganglia, strong contraction and pallor of the uterus and vagina,—or of the vasa deferentia and seminal vesicles—are constantly obtained. Between the 6th and 7th lumbar ganglia, the sympathetic sometimes has a slight effect, sometimes none. Below the 7th lumbar ganglia, we have not found any effect from stimulation of the sympathetic. From this we may fairly conclude that the 3rd, 4th and 5th lumbar nerves send

efferent fibres to the structures in question, and sometimes the 2nd lumbar nerve also.

We have made a certain number of observations both in cat and rabbit, stimulating the lumbar nerves in the vertebral canal. The results we give in the following Tables.

Origin of Efferent Nerve Fibres in the Rabbit.

	Uterus and Vagina.			Vasa Deferentia and Seminal Vesicles.				
Exp.	9	19	25	27	37	23[1]	$\frac{24}{32}$	26
I Lumbar	0	—	—	0	0	—	—	—
II „	?0	—	—	0	0	—	—	—
III „	S	M.G	—	G	S.M	0	—	0
IV „	G	G	G	—	G	G	G	G
V „	G	—	—	—	G	G	—	G
VI „	—	—	—	—	0	0	—	—
Arrangement of Nerves	M	M	P	A	A to M	M to P	P	P

Unless otherwise mentioned both contraction and pallor were observed.

[1] The effect was abolished by cutting the rami to the inferior mesenteric ganglion: though the Vth lumbar still caused some contraction of the bladder.

Origin of Efferent Nerve Fibres in the Cat.

	Uterus.				Vasa Deferentia & Seminal Vesicles.				
Exp.	27[1]	26[2]	9[3]	56	8	59	32	63	64
I Lumbar	0	0	?0	—	—	—	—	0	—
II „	S	?S	?S	—	—	—	—	0.S	0
III „	S.M	S.M	M	—	M	—	—	M	S
IV „	M	M	G	G	—	G	M	G	M
V „	?0	?0	—	M	—	0	0	M	S.M
VI „	—	0	—	0	—	0	0	0	0
Arrangement of Nerves	M	P. (*a*)	Post. (*b*)		Ant.		A to M	M	P (*a*)

[1] After cutting the left hypogastric nerve, the spinal nerves on the left side had no effect.

[2] Pallor observed, but no certain contraction. After cutting the branches to the inf. mes. gang. on the left side, the spinal nerves on that side had no effect.

[3] After cutting both sympathetics between the 7th lumbar and 1st sacral ganglia, the spinal nerves produced their normal effect.

Course of the Lumbar Fibres.

Both in cat and rabbit, the nerve fibres run by the white rami communicantes to the sympathetic, and nearly all of them run then to the inferior mesenteric ganglia. Occasionally a few leave the sympathetic below the 6th lumbar ganglion, and apparently run direct to the pelvic plexus, but we have not found any to come off lower than the 7th lumbar ganglion.

From the inferior mesenteric ganglia they proceed by the hypogastric nerves[1].

In the rabbit, most of the fibres run to the lower pair of the inferior mesenteric ganglia, for whilst stimulation of these gives constantly good effects, stimulation of the upper pair has a much less effect and occasionally none. Moreover it sometimes happens that the upper pair have an effect on the uterus but not on the vagina.

The contraction and pallor go hand in hand in so far that if the upper pair of ganglia have the one effect, they have the other also.

On stimulating separately the peripheral branches of the hypogastric in the pelvic plexus, separate contraction and pallor may be obtained of the vagina and of portions of the uterus on the same side. Anatomically these strands of the pelvic plexus appear to proceed to a certain extent from the pelvic nerve. Since, however, the pelvic nerve does not carry efferent fibres to the uterus (cp. below) the contraction of the uterus which is caused by stimulating the strands of the pelvic plexus can only be due to efferent hypogastric fibres. We have obtained from the three main vesico-uterine strands of the plexus, proceeding from the ventral to the dorsal strand, separate contraction of the vagina, of the basal part of the uterus, and of the terminal half to two-thirds of the uterus on the same side.

In no part of their course have the lumbar nerves, in our experiments, shown any inhibitory or vaso-dilator action on the uterus or vagina or on the vasa deferentia and seminal vesicles.

The Sacral Nerves.

We do not find that stimulation of the sacral nerves, or of the pelvic nerve near its origin, has any direct effect on the uterus or vagina in

[1] Sherrington's remark (*op. cit.* p. 685) that the efferent fibres for the vas deferens run in the genito-crural nerve must, we think, be due to a slip of the pen. The hypogastric always has an effect, but we have never found the peripheral end of the genito-crural to produce any. It does however cause contraction of the cremaster in the dog.

the female, or on the vasa deferentia or seminal vesicles in the male. Sometimes however the strong downward movement of the end of the colon which is caused by the sacral nerves may serve as a mechanical stimulus to the vagina or prostate vesicle and so cause contraction.

Having failed repeatedly to obtain contraction from stimulation of the sacral nerves, we paid especial attention to the question of the presence of inhibitory fibres. In the ordinary quiescent state of the organs, there was no trace to be seen of elongation or flabbiness, when the sacral nerves were stimulated, nor were the rhythmic spontaneous contractions which sometimes occur modified in any appreciable manner.

We tried then, in the rabbit, simultaneous stimulation of the lumbar and sacral fibres: varying strengths of current were used for each nerve; and the stimulus was applied sometimes first to the lumbar and sometimes first to the sacral nerve. In no case did we find that the stimulation of the sacral nerves influenced in any way the effect of stimulating the lumbar nerves.

We give the following extract from an experiment to indicate the general nature of the observation.

Protocol VI. *Rabbit. Simultaneous stimulation of lumbar and sacral nerves.* Right vas deferens observed. Separate tetanising apparatus used for the lumbar and sacral nerves. With the secondary coil at 10 c.m., the shocks were very distinct to the tip of the tongue, but were not strong.

The right 5th lumbar nerve, and the 2nd, 3rd and 4th sacral nerves (tied together), were stimulated for about 20 seconds, the interval between successive stimulations being 1 to 1½ minute; the latter stimulated with a rather strong tetanising current (c. = 8) giving very strong contraction of the bladder; the former with a tetanising current diminishing in strength in the four successive stimulations (viz. c. = 10, c. = 12, c. = 15, c. = 16). In each case normal contraction of the vas deferens was produced.

After this, the sacral nerves were stimulated alone for 10 seconds, then the stimulus was thrown into the 5th lumbar nerve, and both lumbar and sacral stimulated for about 20 seconds. There were four successive stimulations, the position of the secondary coil being constant for the sacral nerve (c. = 8), and being shifted away from the primary coil in the successive stimulations (c. = 10, 12, 15, 16) of the lumbar nerves. The sacral nerves were still entirely without effect on the vas deferens. A cannula was then tied in the vas deferens about the level of Poupart's ligament, and salt solution at a slight pressure kept in it. The sacral nerves caused no alteration in the level of the fluid in the cannula, the 5th lumbar nerve at once drove it up.

Since the view that the sacral nerves send efferent fibres to the uterus is widely accepted, and since we were unable to find any physiological evidence of the existence of such fibres, it seemed to us highly desirable to test the view in another way. To this end we cut in the cat the roots of the sacral nerves in the spinal canal, and after five or more days examined the branches of the pelvic plexus for degenerated fibres. The results have completely carried out our view that no efferent fibres pass from the sacral nerves to the internal generative organs. Since, however, the results throw some light on the innervation of several of the pelvic viscera, and since it is desirable to deal also with the question of the distribution of sensory sacral fibres, we shall consider, in a separate section, the results obtained by the degeneration method.

Contraction of the uterus has been observed to follow stimulation of the central end of a number of sensory nerves. Röhrig found a similar effect from stimulating the central end of the nervus erigens. We have not paid much attention to the reflex effects, but we may mention one point in this connexion. We have sometimes found in the rabbit that section of the sacral nerves or of the pelvic nerve on one side stops the rhythmic contraction of the seminal vesicle on that side, and that contraction could then be obtained by stimulating either the central end of the cut pelvic nerve, or the central end of the cut sacral spinal cord. This implies that afferent impulses ascend the pelvic nerve—not necessarily from the vas deferens itself—and tend to cause a reflex contraction through the lumbar nerves.

SUMMARY.

The internal generative organs with which we are concerned are the Fallopian tubes, uterus, and vagina in the female; the vasa deferentia and seminal vesicles (or the uterus masculinus) in the male; structures developed from either the Müllerian or the Wolffian ducts.

The origin from the spinal cord of the efferent fibres which run to each of these structures is the same.

The usual relative effect of stimulating the several lumbar nerves is as follows:—

	Rabbit	Cat	
		Anterior	Posterior
II Lumbar	0 or ? Slight	Slight	? Slight
III „	Moderate	Good	Moderate
IV „	Good	Good	Good
V „	Mod. to Good	0	Moderate
VI „	0	0	0

The efferent fibres are motor for the muscular walls, and vaso-constrictor for the small arteries. The effect on the uterus and vagina is more constant in the rabbit than in the cat, though in both it varies with the state of the uterus with regard to parturition. In the cat, pallor of the uterus, with little or no contraction, is not infrequently obtained.

Both in the rabbit and the cat, the motor fibres supply the longitudinal as well as the circular muscular coat. This is at times perfectly clear in the uterus, and is always unmistakable in the vasa deferentia.

In the dog, the contraction of the vasa deferentia produced by stimulating the upper set of nerves, is much less than it is in the cat and rabbit; and there is little or no longitudinal contraction. It may be noted that in the cat and rabbit, in which there is strong longitudinal contraction of the vasa deferentia, there is no cremaster muscle, whilst in the dog, in which the longitudinal contraction of the vasa deferentia is slight or absent, the cremaster is well developed.

Unilateral stimulation gives sometimes slight contraction and pallor of the uterus on the opposite side; the crossed action is much less than in the case of the bladder or of the external generative organs.

The course taken by the efferent fibres is the same as that already described for the lumbar fibres to the bladder, except that no fibres for the internal generative organs leave the sympathetic below the 7th lumbar ganglion.

The sacral nerves send neither motor nor inhibitory fibres to any of the internal generative organs.

PART V. POSITION OF THE NERVE CELLS ON THE COURSE OF THE EFFERENT NERVE FIBRES.

WE have seen that there are two sets of nerve fibres to the descending colon, rectum, bladder, and external generative organs; that the origin of these from the spinal cord and their peripheral course have many points in common. Hence instead of considering separately the position of the nerve cells on the course of the fibres to each viscus, we take them here together. The efferent fibres to the internal generative organs we can consider at the same time, although these are contained in the upper set of nerves only.

The Upper Set of Nerve Fibres.

After injection of 10 to 15 milligrams of nicotin into a vein of a rabbit or cat, stimulation of the lumbar nerves in the spinal canal has no effect whatever on the viscera[1]. Hence all the visceral fibres of the lumbar nerves must be connected with nerve cells somewhere in their course. It will be noticed that this holds also for vaso-dilator fibres if such are present. Similarly, stimulation of the sympathetic chain from the 1st to the 6th lumbar ganglion has no effect. Hence the nerve cells are not in this portion of the sympathetic chain, but lie in the more peripheral course of the nerves. In other words, the ganglion cells of the lumbar sympathetic chain (1st to 6th) are not on the direct course of the nerve fibres passing to the descending colon, uterus, bladder, or external generative organs, and the ganglia send no fibres to these viscera. We have seen that from the lumbar sympathetic chain the nerve fibres take two main courses (1) outwards to the inferior mesen-

[1] We may recall that the paralysis produced by a small dose of nicotin rapidly disappears; thus in the rabbit and cat, 10 milligrams of nicotin may cause *complete* paralysis of pre-ganglionic fibres for about a quarter of an hour only. In the dog, complete paralysis is brief even after large doses.

teric ganglia, and (2) downwards in the sympathetic chain. These two courses we will consider separately.

(1) *Course through the mesentery.* The spinal branches to the inferior mesenteric ganglia are, *after injection of nicotin,* as ineffective as the spinal nerves or as the lumbar sympathetic, but on reaching the inferior mesenteric ganglia, all the effects of the upper set of nerves can be obtained, but with varying degrees of strength.

Rabbit. In the rabbit, *stimulation of the ganglia* causes pallor and inhibition of the descending colon—commonly with a brief preliminary contraction—as if no nicotin had been given. Although, no doubt, some of the nerve fibres run through the inferior mesenteric ganglia and end in nerve cells more peripherally, the fibres given off to the descending colon by the ganglia are so numerous as to produce an apparently maximal effect.

The stimulation produces also contraction of the bladder, but it is less than normal, implying that an appreciable number of nerve fibres for the bladder end in cells peripherally of the inferior mesenteric ganglia.

The effect on the uterus and vagina—or vasa deferentia and seminal vesicles—varies considerably in different cases. Usually there is pallor and contraction, though the extent of these varies widely. Sometimes no effect is produced until the hypogastric nerves in some part of their course is stimulated, and this part may be in the peripheral branches close to the uterus. It will be remembered that in the rabbit, nerve cells are often found at short intervals along the course of the hypogastric nerves, where they are joined together, as well as in the peripheral branches. On the whole then we conclude that usually some efferent fibres for the uterus and vagina—and the vasa deferentia and seminal vesicles—end in the inferior mesenteric ganglia, but that many run on to the peripheral nerve cells on the course of the hypogastric nerves; that the number which have the former connection is variable; and that occasionally the efferent fibres all pass by the inferior mesenteric ganglia to join the more peripheral nerve cells.

Further some retraction and pallor may occur in the external generative organs, but it is at best small, and not infrequently we have observed none.

In the rabbit, the upper and lower inferior mesenteric ganglia are often a sufficient distance apart to enable them to be stimulated separately. After nicotin has been given, stimulation of the upper one affects chiefly the descending colon and especially its upper part, it has

a slight effect only on the bladder, it commonly has none on the uterus and vagina; stimulation of the lower one also has an effect on the descending colon but chiefly in its lower part, but it has in addition a marked effect on the bladder and usually some on the uterus and vagina. In fact, the nerve fibres given off by the two ganglia have a somewhat different distribution: both send fibres to the descending colon, but the upper sends more to the upper, and the lower to the lower part; the lower ganglion is the chief source of the fibres for the hypogastric nerves.

After nicotin, then, stimulation of the branches ascending from the ganglia, and of the colonic nerves has its usual effects. The effect of stimulating the hypogastric is diminished on the bladder. It is much more diminished on the lower part of the colon, on the rectum, on the internal and the external generative organs. In some cases, no effect is obtained on the two latter.

Careful local application of warm ·5 to 1 p.c. nicotin to the inferior mesenteric ganglia completes the proof obtained by the injection method, as to the connections of the nerve cells. Care is required in such local application, and caution in interpreting the results, since with a thick ganglion, and with a ganglion having a thick sheath, the nicotin may not penetrate to all the cells, and since an excess of nicotin may annul the irritability of the nerve fibres. When 1 p.c. nicotin is, with due precaution, brushed over the whole surface of the inferior mesenteric ganglia and the nerves in the neighbourhood, peripheral effects can still be obtained by stimulation of the rami to the ganglia. On the intestine the effects are usually very slight, and sometimes we have failed to observe any. On the bladder the effect is obvious, though considerably less than normal. On the uterus and vagina—or vasa deferentia and seminal vesicles—the effects are pronounced though somewhat less than normal.

Cat. In the cat we have made similar experiments both on the effect of injecting nicotin into the blood vessels and of applying it locally to the inferior mesenteric ganglia. The results were essentially the same as in the rabbit, bearing in mind the points in which the cat normally differs from the rabbit. Thus in the cat, the upper set of nerves have frequently no effect on the descending colon except pallor, and the same may be the case with the uterus. Naturally, then, stimulation of the inferior mesenteric ganglia, or of the nerves proceeding from them, may, after nicotin, give pallor of the descending colon and uterus without constant or appreciable contraction. In the

cat, the upper set of nerves normally cause contraction of the internal anal sphincter; after nicotin has been injected, a contraction of the sphincter, though a weaker one, is still obtained by stimulating the hypogastric nerves. Lastly, we may mention that when in the cat, the upper part of the hypogastric nerves has no effect on the vasa deferentia and seminal vesicles—or on the uterus—no effect is, as a rule, produced by stimulating the lower part of these nerves. The effect is only obtained when the electrodes are placed on, or past, one of the peripheral ganglia on the branches of the nerves. This is in harmony with the fact that in the cat the trunk of the hypogastric nerve does not contain nerve cells so commonly as it does in the rabbit.

We have already published some observations[1] made on the cat, with regard to the effect of stimulating the hypogastric nerves after section of the nerves themselves or of the rami to the inferior mesenteric ganglia. The results agree with those obtained by the nicotin method. Degeneration of the nerves running to the inferior mesenteric ganglia diminishes but does not annul the normal action of the colonic and hypogastric nerves proceeding from the ganglia. Section of the hypogastric nerves, time being given for degeneration, annuls all the actions of the peripheral portions of the nerves.

Our conclusions, then, are as follows. The nerve fibres which run from the lumbar nerves to the inferior mesenteric ganglia, run to them direct without having nerve cells on their course.

Nearly all the efferent fibres for the descending colon, whatever their function, end in the cells of the inferior mesenteric ganglia.

In these ganglia end also, a considerable proportion—difficult to estimate with any exactness—of the nerve fibres for the bladder and internal anal sphincter, a smaller variable proportion of the fibres for the internal generative organs; and sometimes a few fibres for the external generative organs.

The rest of the nerve fibres are connected with nerve cells placed more peripherally. Thus a few fibres are connected with nerve cells on the course of the colonic nerves; and a larger number run down the hypogastrics to terminate

[1] Langley and Anderson. This *Journal*, XVI. 410. 1894; XVII. 183. 1894.

in the nerve cells of one or other of the small ganglia, which lie on the branches of the hypogastrics and for the most part near the organs they supply.

(2) *Course by the sacral sympathetic chain.* The other course of the efferent nerves, viz. downwards in the sympathetic chain is taken, as we have seen, chiefly by the nerve fibres to the external generative organs. When, after injection of nicotin, the sympathetic trunk is stimulated more and more posteriorly, the characteristic effects of the upper set of nerves are usually first obtained on stimulating the 1st sacral ganglion in the cat, the 2nd in the rabbit, but occasionally a slight effect may be obtained from the ganglion immediately above these. A stronger effect is obtained from the 2nd and 3rd sacral ganglia in the cat—maximal as a rule from the 2nd; and from the 3rd and 4th sacral and 1st coccygeal in the rabbit—maximal as a rule from the 4th.

Hence then the great majority of the nerve fibres to the external generative organs are connected with nerve cells in the sacral ganglia of the sympathetic chain.

There can be little doubt that the variations which occur in different individuals in the order of effectiveness of the several ganglia are in correspondence with the variation in the arrangement of the sacral nerves. We have found this to be so in a few test cases, but we have not thought it worth while to work the matter out in detail. It must be remembered that in the sacral region the ganglia of two successive nerves may be joined together, so that in such cases the grey rami to the several nerves must be stimulated; otherwise it is sufficient to cut the sympathetic between each two ganglia, and to stimulate the ganglia.

The Lower Set of Nerves.

In considering the effect of nicotin on these nerves we must first put on one side the nerve fibres which belong to the somatic division, and supply the external sphincter of the anus, the bulbo- and ischio-cavernosus muscles and so forth. These nerve fibres have no nerve cells on their course, they resemble ordinary motor nerves to skeletal muscle. The nerve-endings of these nerve fibres are paralysed at about the time the motor nerves to skeletal muscle are paralysed; 15 to 25 milligrams of nicotin are required, *i.e.* 5 to 10 milligrams more than are sufficient to paralyse the connexions of the visceral pre-ganglionic nerves with their nerve cells. Since the movements of the striated muscles tend to

obscure the observation of visceral effects, it is better to give 20 to 25 milligrams of nicotin instead of the smaller dose of 10 to 15 milligrams, or to give curari before nicotin.

Nicotin does not paralyse all the visceral effects which are commonly seen on stimulating the sacral nerves in the spinal canal. It prevents the occurrence of the whole of the effects which the sacral nerves produce through the pelvic plexus, viz. all the effects on the colon, upper part of rectum, and bladder, the inhibition of the internal anal sphincter, of the external generative organs, and of the genito-anal skin muscles. But as we have mentioned earlier (Part III. p. 109) it does not prevent retraction and pallor of the external generative organs, nor contraction of the genito-anal skin muscles. We have shown that this is due to stimulation of the grey rami, joining the nerves from the sacral sympathetic ganglia.

There are one or two other points we may mention here. In the rabbit after nicotin has been given we have not observed any effect on the internal sphincter of the anus, on stimulating the sacral nerves in the spinal canal (cp. Part I. pp. 87, 88). There is however marked contraction of the skin over the end of the rectum. In the cat, we have sometimes observed a slight constriction of the sphincter, and more commonly pallor, apparently due to stimulation of the sacral nerves. We conclude then that few, and sometimes none, of the lumbar fibres for the internal anal sphincter which descend the sympathetic as far as the sacral ganglia (cp. Part I. p. 98) take their further course by the sacral grey rami and the pudic nerves.

The pelvic nerve (nervus erigens) stimulated centrally of its first ganglion, after nicotin injection, has usually no effect; occasionally we have seen a trifling contraction of the bladder, due probably to stimulation of fibres joining the pelvic nerve from the aortic plexus. Stimulation just peripherally of the first ganglion causes weak contraction of the bladder; moderate to strong contraction of the recto-coccygeal muscle and in the rabbit moderate to strong contraction of the rectum also. On stimulating more and more peripherally the several strands of the pelvic plexus, the effects obtained increase in strength, and near each organ a spot can generally be found which gives effects, which are to the eye not greatly less than maximal. The effect of the peripheral branches is least—though it is quite distinct—in the case of the vaso-dilator and inhibitory fibres for the external generative organs; we think this is due partly to the exposure which is unavoidable in dissecting out the branches, and partly to the lowered blood-pressure.

On stimulating the peripheral branches of the pelvic plexus, some ganglia on the course of the hypogastric nerves will naturally be stimulated as well as those on the course of the pelvic nerve fibres. Thus for example contraction of a definite part or of the whole of the uterus may be obtained (cp. Part IV. p. 127).

In the rabbit, the anterior and sometimes the antero-median strand of the pelvic plexus gives contraction of the descending colon, but much less than normal; a stronger but still not maximal contraction can be obtained by stimulating the strand of nerve fibres which ascends in the mesentery ventrally of the hypogastric nerves (cp. Anatomical Part). The central end of the united hypogastric nerves, which normally in the rabbit has an effect on the descending colon, rarely if ever has an effect after nicotin has been given.

On careful local application of nicotin to the first ganglion, whether in rabbit, cat, or dog, the effect of the pelvic nerve on the rectum and recto-coccygeal muscle is decreased to a much greater degree than any other action of the nerve.

Hence then the nerve cells for the several organs are scattered on the course of the nerve strands to them, but most of the nerve cells for any one organ are in ganglia near the organ, thus the first ganglion on the course of the pelvic nerve (nervus erigens), which lies by the side of the rectum, is chiefly for the rectum and recto-coccygeal muscle; the ganglia in the lateral ligament are chiefly for the bladder, the ganglia for the colon are chiefly near the colon, those for the generative organs, close to the urethra or in the organs themselves (cp. later, Anatomical Part).

Effects of large doses of nicotin. The injection of large amounts of nicotin has not given us any constant differences in effects from those produced by small ones. On the whole the motor effects after a large dose have been less marked. On stimulating the hypogastric nerves, the contraction of the bladder was more feeble, the contraction of the uterus or vas deferens was more commonly only obtained by stimulating the peripheral ganglia on the course of the hypogastric, *i.e.* the ganglia of the pelvic plexus; the motor effects on the colon and rectum, on stimulating the inferior mesenteric ganglia, were less commonly seen, so that we were inclined to think that a large dose of nicotin had some paralysing action on motor nerve endings of the post-ganglionic fibres.

But on comparing the details of the several experiments this view

seems to us doubtful[1]. We have obtained in the rabbit strong contraction of the recto-coccygeal muscle from stimulating the posterior branch of the pelvic nerve after 130 milligrams of nicotin; good contraction of the colon from stimulating the sacral colonic nerves and the inferior mesenteric ganglia, after 100 milligrams of nicotin. We have obtained also fair contraction of the vasa deferentia from stimulation of the hypogastric nerves, after injection of 65 milligrams of nicotin. But as the two latter effects, at any rate, have not been obtainable in some cases, after a small dose of nicotin such as 20 milligrams, we think it possible that the observed tendency to enfeeblement of the effects of nerve stimulation is due to normal variations in the responsiveness of the tissues in the several cases, and to variations in the position of the peripheral ganglia. We may mention however that in the rabbit inhibitory effects on the intestine, and vaso-constrictor effects, can be obtained with ease by stimulating the inferior mesenteric ganglia, whatever the amount of nicotin given.

It must be noted, in this connexion, that in most of our experiments, we inject the nicotin immediately after giving anæsthetics, before the nerves are dissected, so that in most cases we do not know exactly the degree of contraction which the nerves are capable of producing before the poisoning. We experiment in this way, partly because nicotin is very apt to cause death if it is given after the intestines have been exposed, and partly because dissection of the nerves may interfere with the circulation, and so lead to a lack of proper distribution of the nicotin when injected.

After large doses of nicotin it is not uncommon to find that stimulation of the sacral nerves, or of the sacral sympathetic ganglia, causes much less retraction of the penis than usual, though it may cause complete pallor. This however appears to be due to the state of retraction into which the penis passes after large doses of nicotin. The more retracted the penis and the less the blood-flow through it, the less obvious will of course be the contractor effects of stimulating the nerves.

The Plexuses of Auerbach and of Meissner. We had hoped that nicotin would enable us to show that some one class of nerves are connected with the nerve cells of the plexuses of Auerbach and Meissner. But this hope failed. For as we have already said, nicotin

[1] Occasionally no effect is obtained for 5 to 10 minutes after the injection of a large dose, but as nicotin throws all visceral nerve cells, and the tissues connected with them, in violent action, the absence of effect is probably due to exhaustion.

in large doses does not paralyse any one of the effects which can be obtained by stimulating the fibres given off by the inferior mesenteric ganglia or by the ganglia of the pelvic plexus. It is true that in most cases, motor effects on the intestine were diminished to a much greater extent than inhibitory or vaso-constrictor effects, but on the other hand the difference was not constant, and it is not unlikely that nicotin should have a slight paralysing action on motor nerve-endings in the intestine.

It is however hardly conceivable that some of the sympathetic nerve fibres should not become connected with the numerous nerve cells which are present in these plexuses, and the observations of Ramon y Cajal, v. Gehuchten, v. Kölliker, and Dogiel show fairly conclusively that such a connexion exists.

We may then, at any rate, conclude that these connexions are of a different nature from those which exist between pre-ganglionic fibres and sympathetic nerve cells; and that the nerve cells of the plexuses of Auerbach and Meissner do not belong to the sympathetic system, but are cells of a different class.

Whenever we have injected pilocarpin after nicotin it has caused strong peristalsis. A small quantity of pilocarpin, *e.g.* 5 milligrams, is sufficient. Direct stimulation also causes ready contraction. In both ways we obtained contraction of the descending colon in the rabbit, after the injection of 130 milligrams of nicotin, although in this particular experiment we failed to obtain any distinct contraction by nerve stimulation.

Action of Curarin. We have made a few experiments with curarin since it has on the superior cervical ganglion an action resembling that of nicotin[1]. The action of curarin differs in several points from that of nicotin; thus curarin paralyses nerve-endings in skeletal muscles more readily than it paralyses the endings of pre-ganglionic fibres in sympathetic nerve cells. We have made four experiments, injecting respectively 20, 40, 100, 110 milligrams of curarin into the jugular. In all its main features the action is the same as that of nicotin though a rather larger amount is required to paralyse the pre-ganglionic fibres. After a large amount, motor effects are perhaps more readily obtained from post-ganglionic fibres, and inhibitory effects perhaps less readily.

[1] Langley and Dickinson. This *Journal*, XI. 516. 1890.