

THE INNERVATION OF THE MUSCULATURE OF THE TONGUE

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THE innervation of the musculature of the tongue has been the subject of much investigation from the histological and physiological points of view. Controversy has ranged around the questions of proprioception and the autonomic innervation of the musculature in this organ. These problems have been reinvestigated by the application of a modified intravital staining method. The results of histological observations made on normal and operated animals have been correlated with clinical findings in man. Nerve stimulation experiments have also been carried out in order to determine the presence or absence of afferent fibres in the hypoglossal nerve.

MATERIAL AND METHODS

The material and experimental procedures which were employed are summarized in Tables I and II.

Table I. *Animal material*

Animals and no. of cases	Muscles studied	Operation	Days allowed for degeneration
34 rats	Intrinsic musculature of tongue	Nil	—
3 rats	Genioglossus and hyo- glossus muscles	Nil	—
2 rats	Intrinsic musculature of tongue	Right hypoglossal nerve cut at base of skull proximal to its junction with branches from superior cervical ganglion	5
3 rats	Do.	Right hypoglossal nerve cut close to its point of entry into the tongue	12
2 rats	Do.	Right cervical sympathetic chain resected	12 and 13
1 rabbit	Do.	Do.	74
1 rat	Do.	Right hypoglossal nerve cut close to the tongue and right cervical sympathetic chain resected	12
1 rat	Do.	Right hypoglossal and lingual nerves cut on the hyoglossus muscle and right cervical sympathetic chain resected	12
1 rat	Do.	Right lingual nerve sectioned	12

Table I (continued)

Animals and no. of cases	Muscles studied	Operation	Days allowed for degeneration
1 rat	Intrinsic musculature of tongue	Right lingual nerve sectioned and right cervical sympathetic chain resected	12
1 rat	—	Stimulation of the right hypoglossal nerve before and after removal of the right superior cervical ganglion	—
1 rat	—	Stimulation of the right hypoglossal nerve. Stimulation of the left hypoglossal nerve after complete isolation from surrounding tissues	—

Table II. *Clinical material*

No. of cases	Nature of experiment	Tests performed		
		Taste on the anterior two-thirds of the tongue by application of cane sugar, common salt and quinine sulphate	Proprioception in the tongue by deformation and stretch	Pain and touch in the anterior two-thirds of the tongue, lower gum and lip, by pin-prick and v. Frey hairs
15	Unilateral and bilateral infiltration of lingual and inferior alveolar nerves with 2% novocain and 0.01% adrenalin	+	+	+
3	Painting surface of tongue with 2% "decicain"	-	+	-
1	Spraying buccal cavity with 5% cocaine	-	+	-
1	Central root section of right trigeminal nerve	-	-	+ including upper lip and gum

STAINING TECHNIQUE

In the course of studies on the innervation of the skin of the ear of the rabbit (Woollard, *et al.* 1939), it was found that nerves could be distinguished *in vivo* after subcutaneous injection with solutions of methylene blue. The staining process is influenced by a variety of factors, chief among which are the concentration and quantity of the dye solution injected and the period elapsing between introduction of the dye and observation of the tissue. Relatively small deviations from the conditions for optimal staining frequently lead to poor results. In the case of the tongue, direct observation *in vivo* cannot be employed, and it becomes necessary to remove the tissue at a suitable time after intramuscular injection of the dye to prepare it for histological examination. The time factor thus assumes greater importance than

in the case of the ear, in which the point of optimal staining can be determined by direct observation.

Experiments. Adult rats under ether anaesthesia were used. A measured quantity of methylene blue solution was injected into the tongue, and after a known period of time the animal was killed by opening the thorax and the tongue excised. The epithelium was removed and thin slices of muscle were transferred to 8% aqueous ammonium molybdate. The specimens, after clearing, were mounted as whole preparations.

The methylene blue solutions were prepared by dissolving the dye in 0.9% sodium chloride solution. On account of the relatively low aqueous solubility of methylene blue at room temperature and the difficulty in detecting undissolved material, care is necessary in preparing solutions of definite strength. This difficulty was overcome by gently warming the dye and saline solution on a water bath for a few minutes and subsequently checking the strength of the solution colorimetrically against a standard solution of the dye. Experiments in which dye solutions prepared at room temperature were compared with solutions which had been heated in the above manner showed that the heating process had no detectable effect on the staining qualities. Although in most experiments B.D.H. methylene blue (Standard Stain) was used, similar results were obtained using "Methylenblau med. pur." of Dr G. Gruebler and Co., Leipzig.

The first three series of experiments were designed to determine the influence on the staining process of the concentration of the dye and the period elapsing between introduction of the stain and removal of the tongue (survival period). The volume injected was 0.65 ml. In the first series of experiments the animals were allowed to survive for 15 min.; in the second series the survival period was 30 min. The concentrations of dye tested were 0.005, 0.01, 0.02 and 0.03%. In all these experiments the staining of nerve was satisfactory, but in certain other respects the results differed considerably. Staining of neurolemma sheath cells, muscle fibres, precipitation and the ingestion of dye particles by macrophages became more marked with increasing concentration in both series. Reticular connective tissue was sometimes stained more markedly when higher concentrations were used. Motor end-plates and fine fibres to blood vessels were well stained by 0.01 and 0.02% solutions of the dye in both series. The best results were obtained using a 0.01% solution of methylene blue with a survival period of 15 min., under which conditions the muscle fibres were only slightly stained, nerves were well stained, motor end-plates showed clearly, and fine fibres to blood vessels were seen in abundance.

The third series of experiments was performed in order to determine whether better results could be obtained by using 0.65 ml. of 0.01% methylene blue solution for a survival period slightly longer or shorter than 15 min. This was not found to be the case.

In a fourth series of experiments smaller volumes were used with a survival

period of 15 min. Concentrations of methylene blue of 0.005, 0.01, 0.02 and 0.03 % in quantities of 0.15 ml. and 0.01 % in quantities of 0.4 ml. were tested. The best results were again obtained with 0.01 % solution.

The results obtained with smaller quantities were, however, inferior to those in which 0.65 ml. were used. In experiments using small volumes it was difficult to observe fine fibres, and it would appear that in order to stain these fibres consistently it is essential to use the larger dose. It was therefore decided in the present investigations to employ 0.01 % solutions of methylene blue in 0.9 % sodium chloride with a survival period of 15 min. Single doses of 0.65 ml. were used. Since only relatively small areas are stained by this amount, 0.65 ml. were introduced into two or more sites when it was desired to study the whole of the musculature of the tongue.

Whilst this technique gives consistently good results for the tongue, suitable modifications must be made when staining nerves in other organs and tissues.

OBSERVATIONS

The innervation of the intrinsic musculature

The intrinsic musculature of the normal tongue is profusely innervated (Pl. I, fig. 1). The bundles of the hypoglossal nerve consist of many thick and a smaller number of thin fibres. Most of the thick fibres on leaving the bundles can be traced to motor end-plates. Others (Pl. I, fig. 2) become gradually thinner, often assume a varicose appearance and finally end on blood vessels (Pl. II, fig. 3). The thin fibres, which are frequently varicose, also end on blood vessels. The motor end-plates never receive more than one nerve fibre (Pl. II, fig. 4), and there are no accessory motor nerve endings. No sensory endings of any kind were seen, nor were any nerve cells observed along the course of the nerve bundles in the tongue.

Circular muscle fibres on arterioles sometimes stain deeply for short distances. The histological picture so produced (Pl. IV, fig. 10) may bear a spurious resemblance to a neuro-muscular spindle (Pl. III, fig. 9; Pl. IV, figs. 11, 12). The true nature of these structures is revealed by the details of their innervation.

Section of the hypoglossal nerve close to the tongue leads to degeneration of all the nerve fibres ending in the muscles and on blood vessels. Section of the hypoglossal nerve at the base of the skull proximal to its junction with branches from the superior cervical ganglion leads to degeneration of the motor fibres but does not affect the nerves supplying the blood vessels. In such a case, the undegenerated sympathetic fibres can be seen coursing among the degenerated fibres of hypoglossal origin (Pl. II, fig. 5). The sympathetic fibres frequently intertwine with one another (Pl. II, fig. 6) whilst on their way to blood vessels. There are no nerve nets. The larger sympathetic fibres have thin myelin sheaths which are lost as the fibres become finer in calibre. Unilateral

removal of the cervical sympathetic chain leads to degeneration of the fibres supplying the blood vessels on the operated side.

Meshworks of fine fibres (Pl. III, fig. 7) are sometimes observed in relation to all the cellular structures present; their configuration suggests a nervous origin. They are, however, devoid of sheaths and cannot be traced into continuity with nerve trunks; moreover, they persist on complete denervation. They are therefore considered to be reticular connective tissue. The arrangement of these fibres bears considerable resemblance to the sympathetic ground plexus, periterminal network and terminal reticulum of some continental authors.

Nerve stimulation experiments

The right hypoglossal nerve was exposed in a rat under light ether anaesthesia. The nerve was stimulated by pinching and by condenser discharges. Stimulation which produced tetanic contraction of the intrinsic and extrinsic musculature of the tongue led to slight dilatation of the right pupil, which rapidly returned to its former size on interruption of the stimulus. The left hypoglossal nerve was then exposed and carefully freed from all surrounding tissues as far as its exit from the base of the skull. During the course of the dissection fine nerve filaments from the region of the superior cervical ganglion to the hypoglossal nerve were severed. Stimulation of the nerve then gave rise to no dilatation of the pupil.

In another rat stimulation of the right hypoglossal nerve gave rise to dilatation of the pupil, but this reaction was not obtained after removal of the right superior cervical ganglion.

Clinical findings

In cases in which the lingual and inferior alveolar nerves were anaesthetized, the area of ageusia was limited to the anterior two-thirds of the tongue and bounded by the midline. The area of anaesthesia to pain and touch was limited by the midline on the tongue and lower lip, but extended for a variable distance as far as the lateral incisor tooth on the lower gum. These findings were confirmed in a case of unilateral central root section of the trigeminal nerve. In this case it was also established that anaesthesia was limited by the midline on the upper gum and lip.

Bilateral anaesthetization of the lingual and inferior alveolar nerves led to the abolition of all forms of sensation tested in the anterior two-thirds of the tongue. The tongue was not, however, ataxic, though articulation was difficult. There was no tendency to bite the tongue. These results were confirmed in the cases in which "decicain" and cocaine were applied to the mucosa.

The clinical results suggested that a certain degree of proprioception might be mediated by sensory endings at the base of the tongue.

The sensory innervation of the extrinsic musculature

The hyoglossus and genioglossus muscles of the rat were examined for sensory nerve endings. These were not found in the fleshy parts of the muscles, but, at the attachment of the genioglossus muscle to the mandible, endings (Pl. III, fig. 8) were found which consist of a thick coil of axis cylinder closely surrounded by enlarged neurolemmal cells. The fibre eventually leaves the coil and, after pursuing a linear course for a short distance, terminates in a small swelling. The configuration of these endings suggest that they respond to changes in tension.

DISCUSSION

Whilst many authors claim to have demonstrated neuro-muscular spindles in the intrinsic and extrinsic muscles of the tongue in animals, in no case is the evidence convincing. The possibility of their existence in man, however, cannot be excluded.

Pilliet (1890), working on a large number of unspecified mammals, found neuro-muscular structures very rarely in sections of the tongue. The author, however, did not differentiate between Pacinian corpuscles and neuro-muscular spindles, and the method of staining is not indicated.

Franqué (1890) records the finding of a muscle spindle with seven muscle fibres in a section of the human tongue. Forster (1894) studied sections of human hyoglossus, genioglossus and omohyoid muscles stained in alum carmine and eosin, and many muscle spindles were stated to occur in these muscles. Schaffer (1922) in his text-book illustrates a transverse section through a muscle spindle in the human tongue.

Langworthy (1924*a*, 1924*b*), using methylene blue, found in the cat, pig, dog, opossum and rat, neuro-muscular spindles in the intrinsic and extrinsic muscles of the tongue. No illustrations of neuro-muscular spindles are given and the criteria for their identification are based on the descriptions given by Sutton (1915) in a study entitled "On the development of the neuro-muscular spindle in the extrinsic eye muscles of the pig." Sutton's figures of methylene blue preparations depict structures similar to stained circular muscle fibres around arterioles. It is now generally accepted that there are no neuro-muscular spindles in the extrinsic ocular muscles.

Tarkhan (1936*a*), examining tongues of rabbits prepared by the method of Bielschowsky, found muscle spindles in the intrinsic musculature of the tongue. Consideration of both the author's photomicrographs and text shows that the preparations did not allow of the identification of the innervation of the structures believed to represent neuro-muscular spindles. The only grounds apparent for the statement that the muscle fibres depicted belong to the class of neuro-muscular spindles is their somewhat fusiform shape and the small diameter of the component muscle fibres. In the absence of the demonstration of the nerve endings the interpretation of fusiform

groups of muscle fibres as neuro-muscular spindles must be accepted with caution.

In contradistinction to the above-mentioned authors, the following workers have recorded the absence of neuro-muscular spindles in the intrinsic muscles of the tongue: Sherrington (1894; cat and monkey; gold chloride and non-specific stains on sections), Batten (1897; man; non-specific stains on sections and Sihler's method on teased preparations), Cipollone (1897; man), Baum (1900; man, numerous mammals, amphibia and fishes; gold chloride and non-specific stains on sections), Boeke (1927; mouse, rat and hedgehog; Bielschowsky's silver impregnation), Hewer (1935; human foetuses; silver pyridine), Boyd (1937; adult and foetal rabbits; various silver methods and methylene blue), Carleton (1937; rabbit, chameleon and ant-eater; pyridine silver), and Lhamon *et al.* (1938; cat).

The anatomical demonstration of sympathetic fibres in the hypoglossal nerve passing to the blood vessels of the tongue corroborates the physiological observations of Morat (1930), who established that stimulation of the hypoglossal nerve leads to vaso-constriction in the tongue, a phenomenon abolished by removal of the superior cervical ganglion. A parallel can thus be drawn between the vasomotor nerve supplies to the tongue and the extremities, in which the sympathetic fibres reach their destination by coursing with the motor and sensory nerves (Woollard, 1926; Woollard & Phillips, 1932).

The intertwinings between sympathetic fibres are suggestive of those occurring between nerve fibres in coelenterates (Schaefer, 1878; Woollard & Harpman, 1939), where they have been ascribed a synaptic significance.

The finding of thin myelin sheaths on the larger sympathetic fibres in the hypoglossal nerve is in accordance with the work of Billingsley & Ranson (1918), Heinbecker & Bishop (1931) and Cleveland (1932), all of whom found myelinated fibres in the post-ganglionic branches of the superior cervical ganglion.

The present observations on the tongue as well as a study of methylene blue and gold chloride preparations of the muscles of the face, mastication, limbs and intercostal spaces in rabbits and cats confirm the findings of Woollard (1927), Wilkinson (1930), Hinsey (1930) and others in denying the existence of the accessory sympathetic innervation to striated muscles described by Boeke (1927), Agduhr (1919) and others. Woollard included in his studies the intrinsic musculature of the tongue of rats, cats and rabbits stained with methylene blue and gold chloride. The present investigations have also failed to disclose the accessory epilemmal motor plaques believed by Boeke (1913) and Langworthy (1924*b*) to be the endings of fibres contained in the chorda tympani nerve.

A fine network of argyrophil fibres has been described by Boeke (1933-6), Stoehr (1934-5), Reiser (1932, 1933) and Sunder-Plassmann (1930-5) in every tissue of the body and is believed by them to be part of the sympathetic nervous system. The nervous nature of this tissue, however, cannot be con-

sidered to have been established, since it has not been shown to disappear on complete denervation. Nonidez (1936, 1937) has shown in silver preparations that the fibres of the network in question are continuous with collagenous fibres, and considers them to be reticular connective tissue. This interpretation is in agreement with the present observations. The authors who describe so-called networks of nervous origin demonstrate their presence by the use of the Bielschowsky silver method, which does not select between nerve fibres and reticular connective tissue (Beech & Davenport, 1933).

Tarkhan (1936*b*) obtained in chloralosed cats a rise in blood pressure on faradization or pinching of the hypoglossal nerve. Acheson *et al.* (1936) recorded in urethanized cats a rise in blood pressure and slight contraction of the nictitating membrane on faradic stimulation of the central end of the cut hypoglossal nerve. Downman (1939) observed dilatation of the pupil in chloralosed cats and dilatation of the pupil, rise in blood pressure and muscular movements in decerebrate cats on pinching and on faradic stimulation of the hypoglossal nerve; the reactions could still be obtained after removal of the superior cervical ganglion. These experiments have been adduced as evidence for the existence of afferent fibres in the hypoglossal nerve. Dilatation of the pupil on stimulation of afferent somatic and autonomic nerves may be due to central inhibition of the oculomotor nucleus (Bain *et al.* 1934, 1935), or the impulse may reach the eye by travelling in the cervical sympathetic chain (Luchsinger, 1880; Anderson, 1904). The experiments on the hypoglossal nerve in rats recorded in the present paper suggest that the impulses reached the pupil via the cervical sympathetic system. The mechanism in these experiments might be explained by the occurrence of local reflexes such as Schwartz (1934) has demonstrated in the autonomic nervous system. Dilatation of the pupil, contraction of the nictitating membrane or rise in blood pressure as indices of afferent impulses must be accepted with caution. Acheson and his collaborators obtained contraction of the nictitating membrane and a rise in blood pressure on faradic stimulation of the hypoglossal, saphenous, "hamstring", splanchnic, hypogastric, hepatic, cervical sympathetic, pelvic and cardiac sympathetic nerves, but faradic stimulation of the cornea, while eliciting a rise in blood pressure, failed to produce contraction of the nictitating membrane. Langworthy (1924*b*) found no Sherrington "pain reaction" on faradization of the hypoglossal nerve in decerebrate cats. Barron (1936), in cats, rats and rabbits either decerebrate or under urethane or sodium amytal anaesthesia, was unable to record action potentials from the hypoglossal nerve on stretching, deforming or burning the tongue. Chemical destruction also gave negative results. Corbin & Harrison (1938), working with cats under pentobarbital sodium anaesthesia, failed to record action potentials indicative of proprioceptive impulses from the hypoglossal, lingual or upper cervical nerves on stretching or twisting the tongue. Downman obtained no dilatation of the pupil or rise in blood pressure in cats in which the chorda tympani, lingual and glossopharyngeal nerves had been cut on pinching, crushing or

burning the tongue, nor on stretching to the extent of tearing the muscle fibres. The author believes that the failure to obtain reflex responses in these experiments can be accounted for by the inadequacy of the stimuli employed. Such an interpretation is not in accordance with physiological experience, since reflex responses and action currents can be elicited by gentle pressure on, or stretching of, muscles known to contain sensory nerve endings.

Carleton (1937) painted the mucosa of the tongue and buccal cavity with 5–10% cocaine in eight subjects. In four subjects the only sensation that could be aroused was one of traction at the base of the tongue. In the remaining four individuals the sense of position did not wholly disappear, possibly because of incomplete loss of tactile sensation, due, the author suggests, to inadequate anaesthetization. The results of Carleton's as well as the present series of clinical observations can be explained by the presence of sensory endings at the origin of the genioglossus muscle.

The sensory overlap found in the region of the lower gum is in accordance with similar clinical findings of Stewart & Wilson (1928). The overlap is explained by the finding of anastomotic fibres at the symphysis in dissections of human material (Starkie & Stewart, 1931). Sensory overlap in the midline has not been found anywhere else in the body.

Matthews (1933) infers from action-potential studies that neuro-muscular spindles, by virtue of their "flower spray" endings, are stimulated by passive stretch of the muscle, and cease to discharge during active contraction of either the surrounding or the intrafusal muscle fibres. The "annulo-spiral" endings are considered to act similarly except that when the intrafusal muscle fibres contract the rate of discharge increases. There would thus appear to be no necessity for structures endowed with "flower spray" endings in muscles that have no postural antagonists. This interpretation is in accordance with the fact that no neuro-muscular spindles can be demonstrated in the striated musculature of the larynx, pharynx and oesophagus, the diaphragm, the bulbo- and ischio-cavernosus muscles (Sherrington, 1897; Schaffer, 1922) and the muscles of the face. The extrinsic muscles of the eye are apparently the exception to this generalization, since they are now generally considered to contain no neuro-muscular spindles. The "terminaisons en grappe" that have been described by Woollard (1927, 1937) and others in the extrinsic ocular muscles, however, are similar to "flower spray" endings and probably subserve the same function. The tongue also has no postural antagonists, and thus it is not surprising that it has no neuro-muscular spindles.

Matthews (1933) concludes that neuro-tendinous endings respond to either passive stretch or active contraction. They are presumed to be the tension recorders "par excellence" (Fulton, 1938). Sensory endings have been found at the insertion of the genioglossus muscle. They are similar to the "ball-like" nerve terminations described by Stoehr (1932*a, b*) in the pia mater and considered to record changes in tension. Although this type of ending differs morphologically from the neuro-tendinous endings of Golgi, it probably sub-

serves similar functions. The origin of the nerve fibres supplying the sensory endings at the origin of the genioglossus muscle has not been determined.

In the extrinsic muscles of the eye the functions of the "annulo-spiral" ending of neuro-muscular spindles may be subserved by neuro-tendinous organs which, though smaller (Sherrington, 1897), closely resemble the tendon nerve endings of Golgi.

SUMMARY

1. The innervation of the intrinsic and extrinsic musculature of the tongue has been studied histologically by a modified methylene blue technique in a series of thirty-seven normal and eleven operated rats and one rabbit in which the hypoglossal and lingual nerves and the cervical sympathetic chain had been resected alone or in various combinations.

2. The staining technique is based upon the injection of measured quantities of solutions of methylene blue in normal saline into tissues in which the circulation is maintained. The method described is applicable to the musculature of the tongue in rats and rabbits and the skin of the ear in the rabbit.

3. No sensory endings were found in the intrinsic muscles of the tongue.

4. No neuro-muscular spindles were found in the hyoglossus or genioglossus muscle.

5. Sensory endings of a tension-recording type were found at the origin of the genioglossus muscle.

6. No nerve cells were found along the course of the hypoglossal nerve in the tongue.

7. Sympathetic fibres run in the hypoglossal nerve to reach the blood vessels of the tongue.

8. No accessory nerve endings to muscle fibres or motor end-plates were found.

9. The sympathetic ground plexus, periterminal network and terminal reticulum are considered to be reticular connective tissue. No nerve nets were observed.

10. Dilatation of the pupil on stimulation of the hypoglossal nerve in rats under light ether anaesthesia was found to be due to stimulation of the sympathetic fibres in the hypoglossal nerve.

11. Proprioception, taste, pain and touch were tested on the tongue, lower gum and lip in nineteen human subjects in which the lingual and inferior alveolar nerves had been unilaterally or bilaterally infiltrated with novocain, or in which the mucosa of the tongue, oral pharynx and palate had been painted with "decicain" or cocaine.

12. In cases in which the lingual nerve was anaesthetized by infiltration the area of ageusia was limited to the anterior two-thirds of the tongue and there was no overlap in the midline.

13. Pain and touch were found to overlap in the midline in the region of the lower gum. This was confirmed in a case of central root division of the trigeminal nerve.

14. All forms of sensation tested in the anterior two-thirds of the tongue were found to be abolished on complete anaesthetization.

15. There was no ataxia or tendency to bite the tongue after complete anaesthetization, although articulation was difficult.

16. The mechanism of proprioception is discussed in the light of the anatomical and clinical findings and recent physiological work.

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EXPLANATIONS OF PLATES I-IV

All the figures are photomicrographs from methylene blue preparations.

PLATE I

- Fig. 1. Rat. Normal. Intrinsic musculature of tongue. Thick motor nerve fibres; thin autonomic nerve fibres. $\times 80$.
 Fig. 2. Rat. Normal. Intrinsic musculature of tongue. Sympathetic fibre (arrows) emerging from a fasciculus of the hypoglossal nerve. The fibre becomes gradually thinner and eventually ends on a blood vessel. $\times 430$.

PLATE II

- Fig. 3. Rat. Hypoglossal nerve sectioned at base of skull prior to its junction with branches from the superior cervical ganglion. Intrinsic musculature of tongue. Termination on a capillary of a sympathetic fibre conveyed by the hypoglossal nerve. $\times 530$.
 Fig. 4. Rat. Normal. Intrinsic musculature of tongue. Motor end-plate. There are no accessory fibres. $\times 530$.
 Fig. 5. Rat. Hypoglossal nerve cut at base of skull proximal to its junction with branches from the superior cervical ganglion. Three sympathetic fibres among degenerated motor fibres in a fasciculus of the hypoglossal nerve in the tongue. $\times 580$.
 Fig. 6. Rat. Hypoglossal nerve cut at base of skull proximal to its junction with branches from the superior cervical ganglion. Intrinsic musculature of tongue. An intertwining between two varicose sympathetic fibres. $\times 725$.

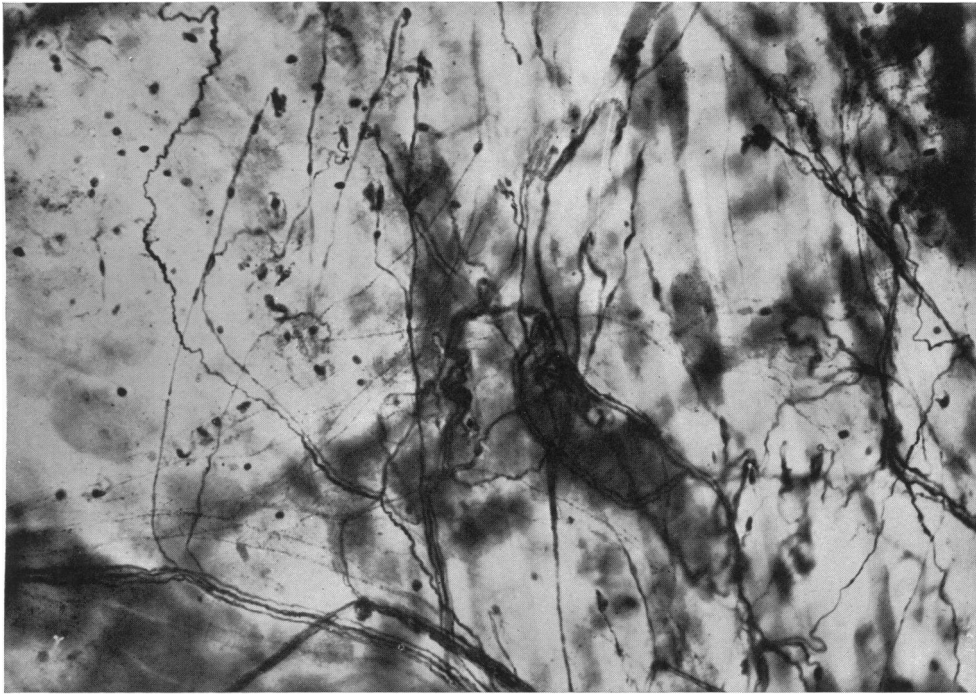


Fig. 1.

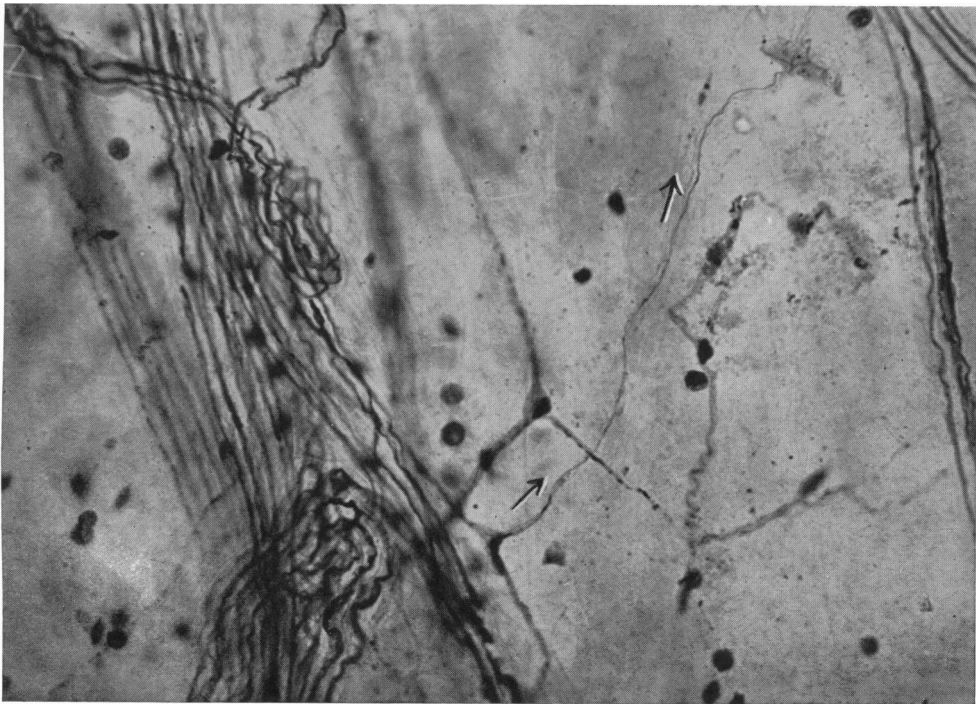


Fig. 2.

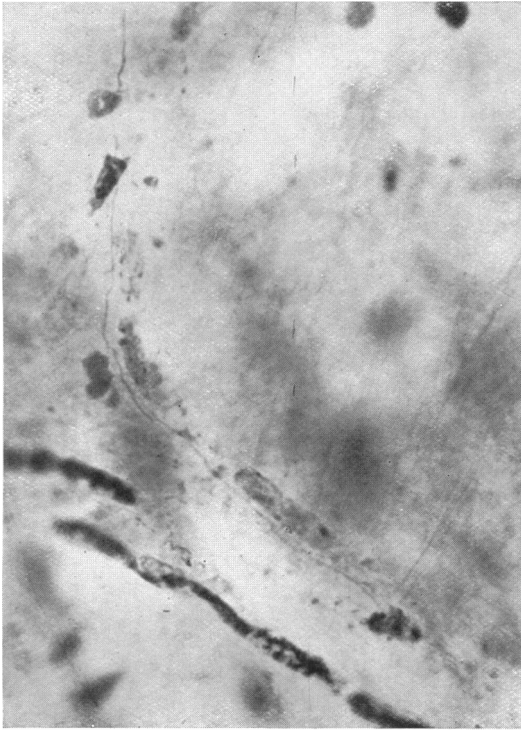


Fig. 3.

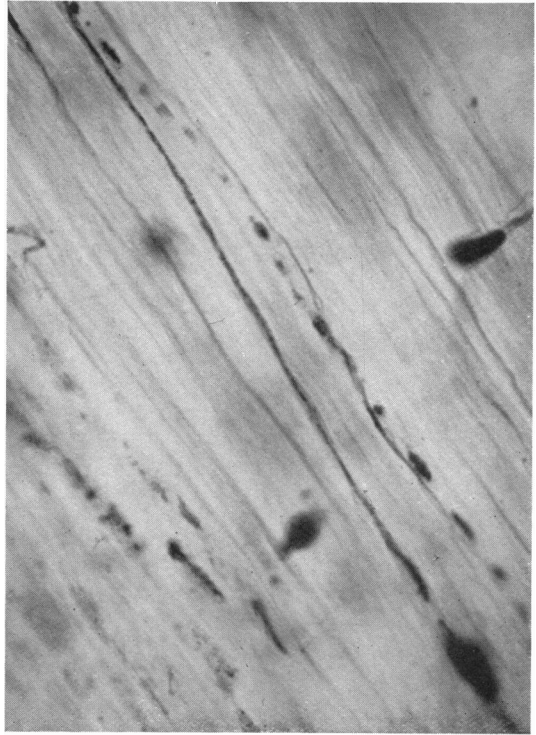


Fig. 5.

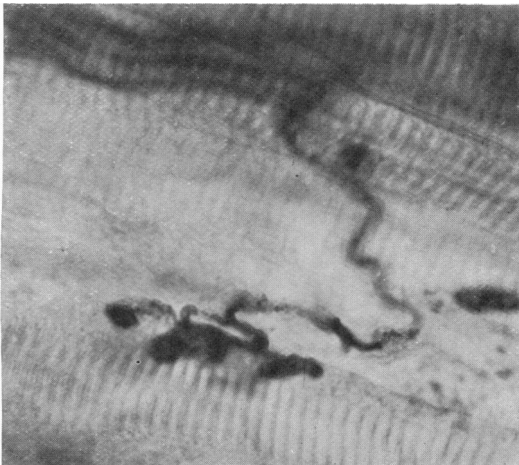


Fig. 4.

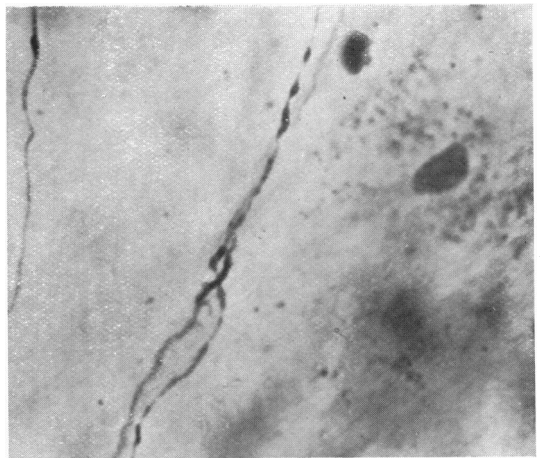


Fig. 6.

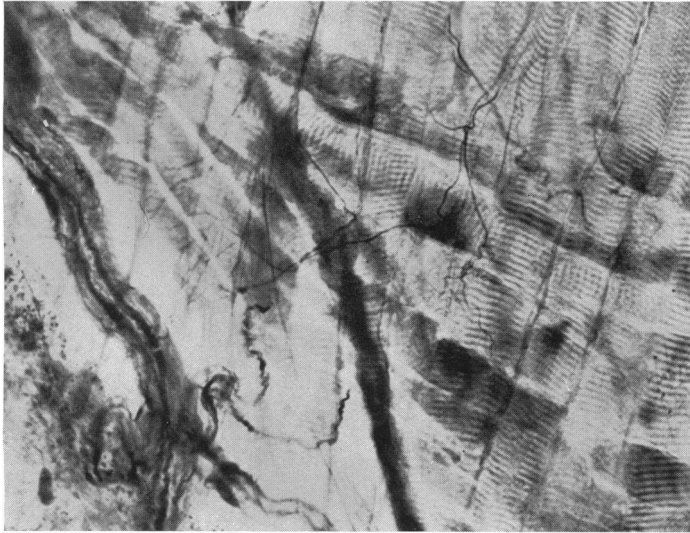


Fig. 7.

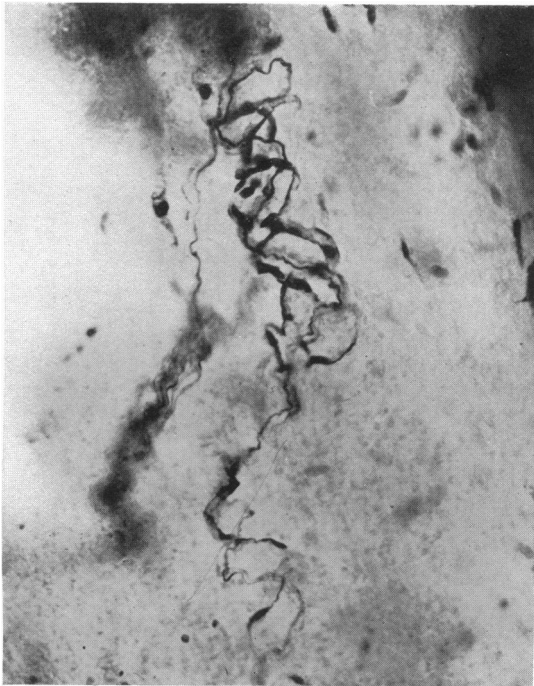


Fig. 8.

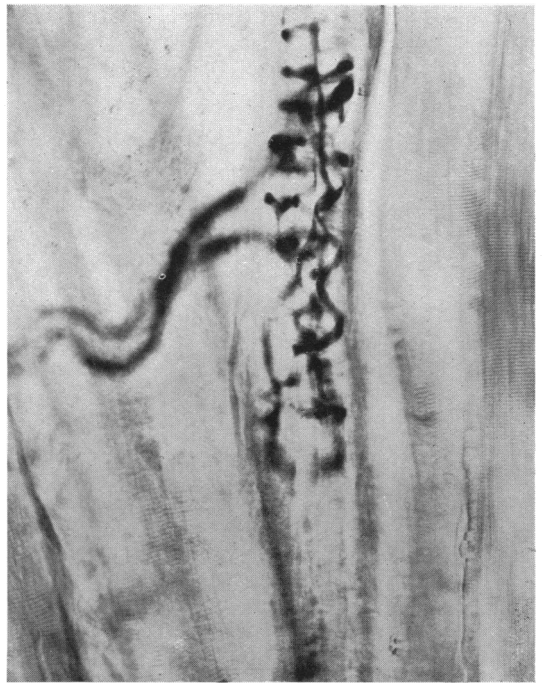


Fig. 9.

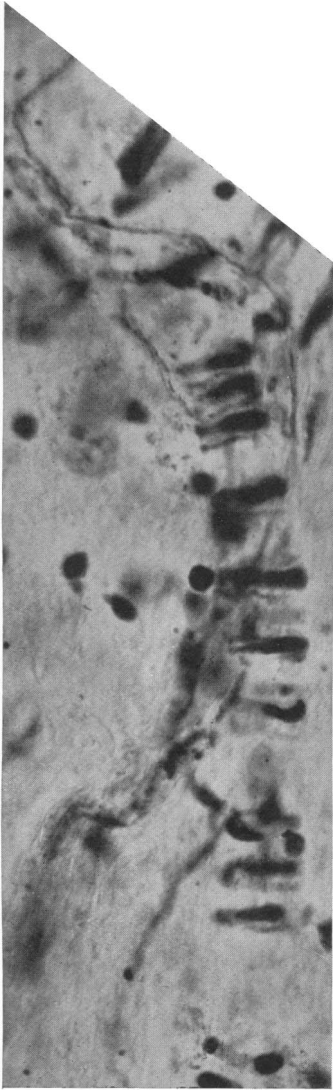


Fig. 10.

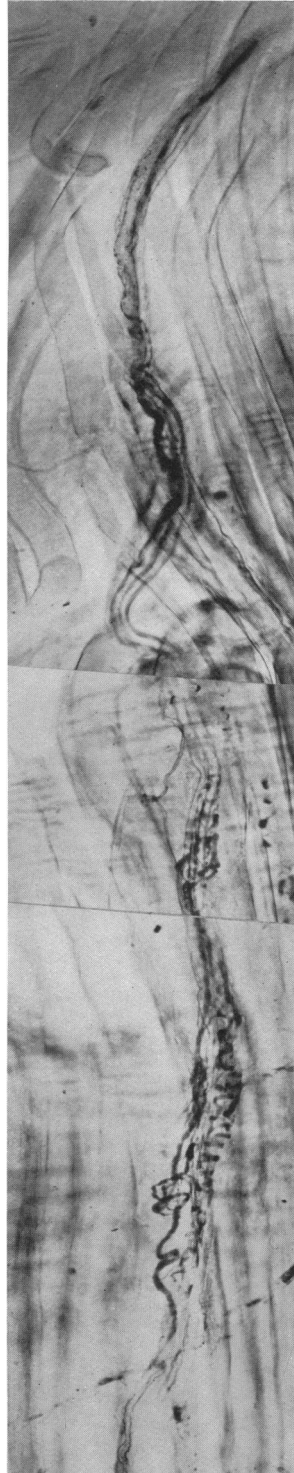


Fig. 11.

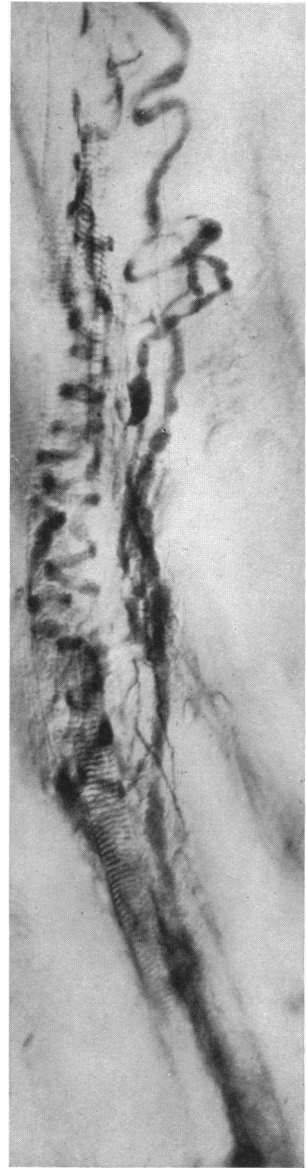


Fig. 12.

PLATE III

- Fig. 7. Rat. Normal. Intrinsic musculature of tongue. Reticular connective tissue fibres. $\times 250$.
Fig. 8. Rat. Normal. Region of attachment of genioglossus muscle to the mandible. A sensory ending of tension recording type. $\times 120$.
Fig. 9. Rabbit. Leg. Extensor digitorum longus muscle. Annulo-spiral ending of a neuro-muscular spindle. $\times 440$.

PLATE IV

- Fig. 10. Rat. Hypoglossal nerve cut at base of skull proximal to its junction with branches from the cervical ganglion. Intrinsic musculature of tongue. Stained circular muscle fibres around an arteriole and nerves supplying the vessel. $\times 440$.
Fig. 11. Rabbit. Leg. Extensor digitorum longus muscle. Neuro-muscular spindle showing the characteristic innervation, shape, length and type of muscle fibre. $\times 220$.
Fig. 12. The annulo-spiral ending of the neuro-muscular spindle illustrated in Fig. 11 seen in more detail. $\times 440$.