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The structure and source of lingual proprioceptors in the monkey

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INTRODUCTION

Lingual proprioception is a problem of long standing. It is a dual problem because of uncertainty surrounding both the nature of lingual proprioceptors and the manner of their connexion with the brain.

It is now well established that muscle spindles exist in the intrinsic and extrinsic lingual muscles of man (Nakayama, 1944; Cooper, 1953; Walker & Rajagopal, 1959; Kubota, Negishi & Nasegi, 1975) and of monkeys (Bowman, 1968). It has not hitherto been shown whether tendon endings or any of the other proprioceptors characteristic of skeletal muscle are present in the primate tongue. In lower mammals lingual proprioceptors are scarce and are simple in form (Weddell, Harpman, Lambley & Young, 1940; Law, 1954).

The source of proprioceptive afferents to the mammalian tongue has not been unequivocally established for any species, and possibly it varies in detail from one species to another. Cooper (1954) and Morimoto & Kawamura (1971) recorded afferent activity in the hypoglossal nerve (HN) of the cat, and various reflex effects have been elicited by stimulation of the central cut end of the cat HN trunk (Downman, 1939; Kawamura, Funakoshi, Nishiyama & Majima, 1965; Kawamura, Funakoshi, Nishiyama & Morimoto, 1967; Nakamura, Goldberg, Mizuno & Clemente, 1970); some, at least, involve a linkage with the vagus (Sauerland & Mizuno, 1968; Hanson & Widén, 1970; Zapata & Torrealba, 1971).

Yee, Harrison & Corbin (1939) observed degenerating fibres in the rabbit HN after removal of the dorsal root ganglion of Cl spinal nerve. The possible existence of a dorsal root ganglion proper to HN has been adverted to ever since Froriep & Beck (1895) described small ganglia on the emerging rootlets of the nerve in several mammals. Langworthy (1924*a*, *b*) and Holliger (1955) found such ganglia in cats, but Boyd (1937, 1941) and Kimmel (1940) could not find them in rabbits. Pearson examined human embryonic (1939, 1943) and adult (1945) material and described 'sensory type neurons' along the intramedullary portion of HN. Tarkhan (1936*a*, *b*) and Tarkhan & Abd-el-Malek (1950) found a variable number of ganglion cells along the extracranial HN trunk in man, dog, cat, and rabbit, and Wozniak & Young (1968) did so in man.

In rhesus monkeys Bowman & Combs (1968, 1969) recorded afferent impulses in the distal HN on stretching the tongue, and potentials were evoked in the sensorimotor cortex. They concluded that spindle afferents present in the distal

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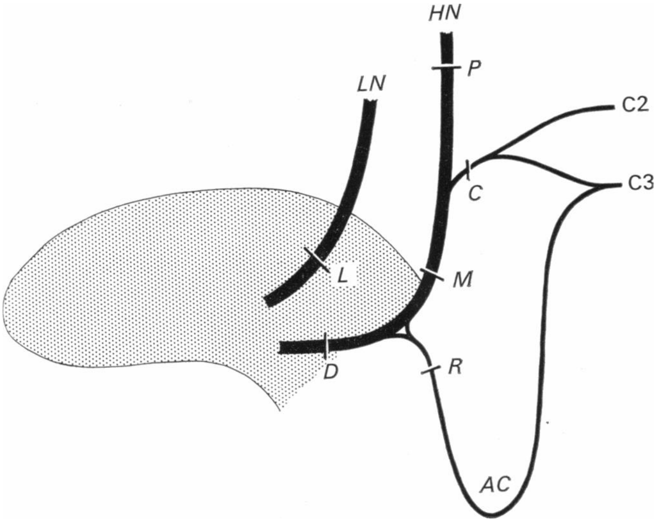


Fig. 1. Sites of nerve section. *L*, section of lingual nerve (*LN*); *P*, *M*, *D*, proximal, mid-, distal section of hypoglossal nerve (*HN*); *AC*, ansa cervicalis; *C*, common trunk from C2–33 ventral rami; *R*, ramus descendens hypoglossi.

HN entered the spinal cord via C2 and C3 dorsal rami. Moreover, HN contained a greater number of large diameter fibres (in which category spindle primary afferents would presumably be included) below the level of junction of the C2–C3 common trunk with the nerve than above that level (Egel, Bowman & Combs, 1968).

The present work was undertaken in order to obtain a more complete picture of proprioceptive lingual innervation in a primate, and to determine its source in a direct manner, by studying degeneration after nerve section.

MATERIAL AND METHODS

Fifteen Cynamolgus monkeys (Shamrock Farms Ltd., Henfield, Sussex, England) were used. Twelve were mature (1·6–3·0 kg, 2–4 years old). Three were young (0·75–1·3 kg, 8–18 months old), having been chosen in order to procure smaller tissue blocks. The nerve sections were carried out on the left side under nembutal anaesthesia, with the aid of a Zeiss operating microscope. In short term survival experiments (2–4 days) the selected nerves were simply sectioned. For longer survival (10–14 days) the proximal stumps were turned aside in order to impede regeneration of nerve fibres into the tongue.

The following procedures (Fig. 1) were carried out through a 2–3 cm skin incision medial to the angle of the mandible (the code numbers refer to post-operative survival in days): (*a*) Lingual nerve section (L4, L10): The mylohyoid muscle was reflected and a hook passed around the trunk of the nerve where it descended onto the hyoglossus. The nerve was severed on the hook. (*b*) Distal hypoglossal nerve section (DH2, 2DH2, DH10, 2DH10, i.e. two 2 day and two 10 day survivals): The mylohyoid was reflected and a hook passed around the hypoglossal nerve distal to the origin of its branches to geniohyoid and thyrohyoid. The hook was slid distally, closing the fan of terminal branches entering the tongue; the nerve was

Table 1. *Details of animals and histological methods*

Code	Wt (kg) and sex	Anterior quarter: plane, stain	Middle half: plane, stain	Posterior quarter: plane, stain
L4	2·6 F	Coronal de C.*	Horiz. G-B‡	Horiz. G-B
L10	3·0 M	Coronal DI†	Horiz. G-B	Coronal DI
DH2	2·2 F	Coronal DI	Horiz. G-B	Horiz. G-B
2DH2	0·75 F	Coronal de C.	Horiz. G-B	Coronal de C.
DH10	2·1 F	Coronal DI	Horiz. G-B	Coronal G-B
2DH10	1·0 M	Coronal DI	Horiz. G-B	Horiz. G-B
MH2	2·5 M	Coronal DI	Horiz. G-B	Coronal DI
MH10	2·5 M	Horiz. G-B	Horiz. G-B	Coronal DI
PH10	2·0 M	Coronal DI	Horiz. G-B	Coronal DI
PHL10	2·5 M	Coronal DI	Horiz. G-B	Coronal DI
C2	3·0 M	Coronal DI	Horiz. G-B	Coronal DI
C10	2·5 M	Coronal DI	Horiz. G-B	Coronal DI
R14	1·3 F	Coronal de C.	Horiz. G-B	Coronal de C.
CR10	2·4 F	Coronal de C.	Horiz. G-B	Coronal de C.
CR14	1·6 F	Coronal G-B	Horiz. G-B	Coronal G-B

* de Castro. † Double impregnation. ‡ Gros–Bielschowsky.

severed on the hook. (*c*) Mid-hypoglossal nerve section (MH2, MH10): The submandibular gland was retracted and the hypoglossal nerve was exposed deep to the angle of the mandible. It was lifted on a hook and severed. (*d*) Proximal hypoglossal nerve section (PH10): The hypoglossal nerve was grasped with fine, curved forceps close to the skull base and was transected above the forceps. (*e*) Procedures (*a*) and (*d*) combined (PHL10). (*f*) Cervical nerve section (C2, C10): The hypoglossal nerve was followed cranially to where it enters into relationship with the internal carotid artery and internal jugular vein, and where its posterior aspect is joined by a stout common trunk formed by the union of branches from C2 and C3 ventral rami. The hook was passed to the cranial side of the connexion, which was pulled down and severed. (*g*) Section of the ramus descendens hypoglossi (R14): The nerve was attached to the hypoglossal deep to the angle of the mandible; it was severed 5 mm below the attachment, which was invariably Y-shaped. (*h*) Procedures (*f*) and (*g*) combined (CR10, CR14). In the course of procedures (*f*), (*g*) and (*h*), in which degeneration of intralingual axons was expected to be slight, sham operations were performed on the right side in each case, the relevant nerves being exposed but not cut.

Animals were killed by bilateral carotid perfusion with 50 ml 0·9 % NaCl, followed by 200–400 ml 4 % paraformaldehyde–sucrose (Richardson, 1960). The middle half of the tongue was later sectioned completely at 30–50 μm and processed by a Gros–Bielschowsky method (FitzGerald, 1963). The anterior and posterior quarters were processed completely (Table 1) either by (*a*) the same method, by (*b*) de Castro's (1925) block silver method, or by (*c*) double impregnation of paraffin sections with silver nitrate and protargol (FitzGerald, 1964). In R14 the ramus descendens on each side was fixed in *s*-collidine-buffered 2 % osmium tetroxide and examined in transverse paraffin and Araldite sections.

The brain stem was removed from DH10, 2DH10, R14 and CR14. Serial paraffin sections at 10 μm were prepared from the medulla oblongata (cut transversely) and from the mid-brain and upper pons (cut in the plane of the cerebral aqueduct, to

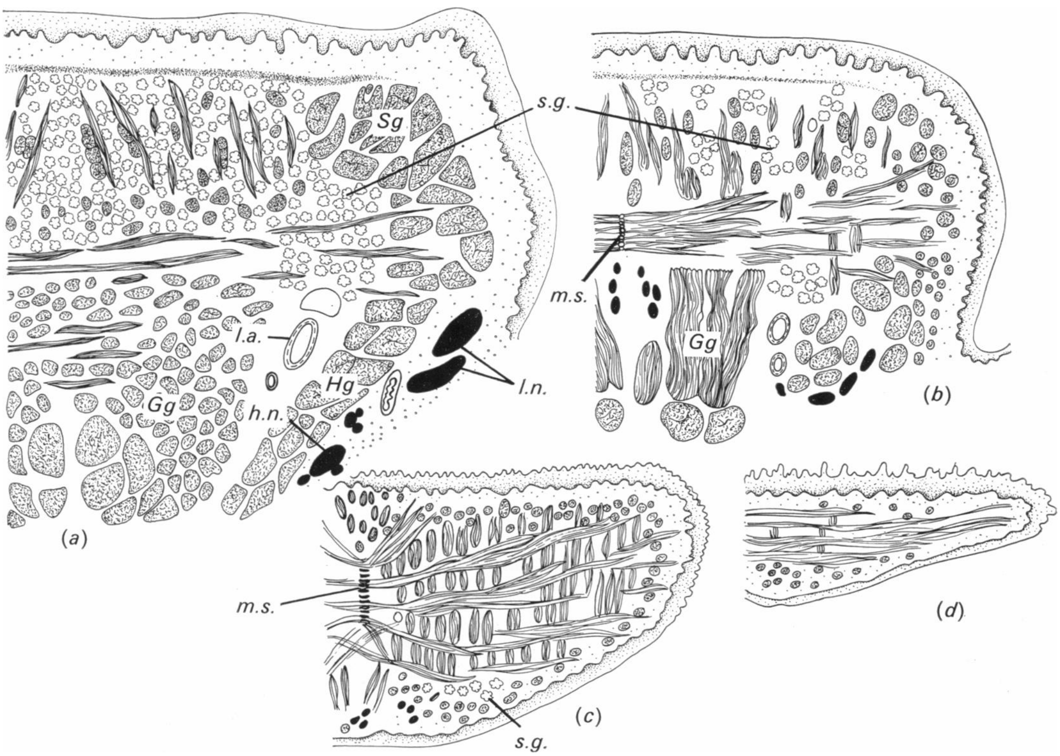


Fig. 2. Representative coronal sections of right side of tongue (including mid-line), from posterior quarter (*a*) to anterior quarter (*d*). *Gg*, genioglossus; *Hg*, hyoglossus; *h.n.*, hypoglossal nerve; *l.a.*, lingual artery; *l.n.*, lingual nerve; *m.s.*, median septum; *s.g.*, salivary glands; Sg, styloglossus.

include both mesencephalic nuclei). The sections were stained with alcian blue–methyl green–pyronin (Mitchell, 1971) for Nissl bodies.

RESULTS

The adult tongue was about 6 cm in length. The median fibrous septum was about 3 cm long, being absent from the posterior 2·5 cm and tapering to end about 0·5 cm from the tip (Fig. 2). Above the septum the mid-line was not demarcated, and behind it the two genioglossus muscles were separated by thin connective tissue. Below its posterior part the medial divisions of the two hypoglossal nerves came into contact, although they were never seen to communicate. Below the anterior part of the septum, bundles of left and right transversus linguae muscles intersected, and small vessels and nerves crossed the mid-line. At the tip of the tongue transversus linguae crossed the mid-line without interruption.

Proprioceptors

Muscle spindles. Muscle spindles were found in the intrinsic and extrinsic muscles of all the animals. Their principal features are compared with those of lumbrical spindles in Table 2. All the lingual spindles were small, the capsules of about

Table 2. *Lingual and lumbrical muscle spindles compared*

	Lingual	Lumbrical
Total length	1–2 mm	2–4 mm
Muscle fibre no.	2–14	4–22
Nuclear bags	Rare	Constant
Round-nuclear chains	Common	Constant
Dolichonuclear chains	Constant	Absent

90 % of them being 0·4–0·6 mm in length, and the intrafusal muscle fibres extending for a similar distance beyond each spindle pole. Some 75 % of the lingual spindles contained four to eight intrafusal muscle fibres (Figs. 4, 7, 8); numbers in excess of 10 were rare, only one having as many as 14. Spindles with two or three fibres were not uncommon (Figs. 3, 5).

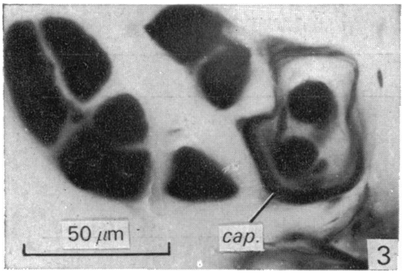
Examination of the equatorial nuclei of several hundred spindles showed two distinct nuclear types, spherical and elongated (Figs. 10, 11, 13). Spherical nuclei (diameter 6–7 μm) were found in the classical nuclear bag fibres. Nuclear bags were rare, not more than ten typical examples being found in the entire series. Spherical nuclei were found also in the occasional intermediate fibres, and in the commonly occurring nuclear chains of classical type. The round-celled chain fibres differed from intermediate fibres only in being more slender, and several transitional examples were found with double and single nuclear rows within the same equator (Fig. 10).

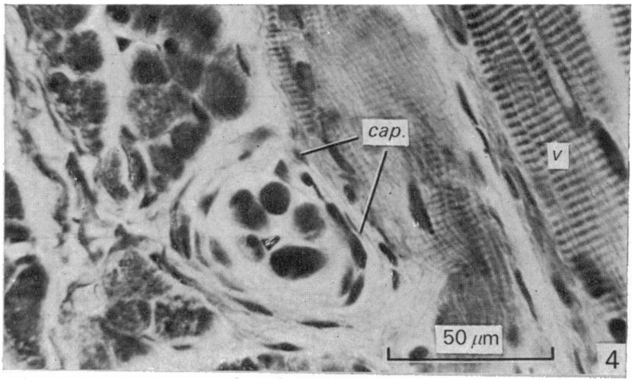
Dolichonuclear (i.e. long-nuclear) chains were found in every spindle. Nuclear length was at least double the nuclear diameter; in many instances the length was more than five times the diameter, extreme examples measuring 80 × 5 μm. Although the nuclear morphology was most clearly seen in denervated spindle equators, the same dichotomy of nuclear types was found on the control side of the tongue. Measurements of sarcomere lengths showed that nuclear shape was not determined by the state of contraction of the intrafusal fibres after fixation (Fig. 13).

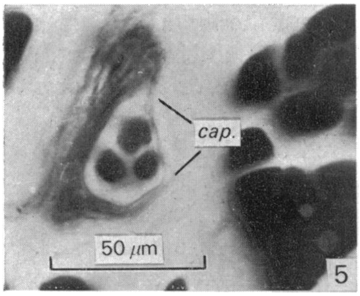
True nuclear chains in the tongue had to be distinguished from nuclear rows observable at the surface of many extrafusal fibres. Sarcomeres were reduced or absent between these nuclei (Fig. 6), and the appearances were suggestive of immature myotubes, although the nuclear rows were detectable in both adult and young animals.

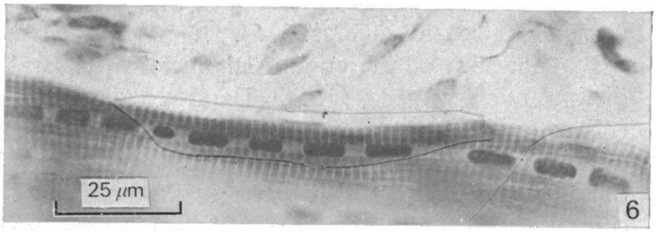
Comparison of the pattern of innervation of lingual and lumbrical spindles revealed no significant differences. The sensory innervation of lingual spindles appeared to be a scaled-down version of the lumbrical pattern. In the lumbricals the primary afferents were relatively coarse and the annulospiral endings more extensive, staining heavily with silver. In the tongue, secondary endings were found only in a few of the largest spindles. The pattern of fusimotor innervation was similar in lumbricals and tongue. Trail endings were smaller in the tongue, but were frequently seen, even in very small spindles. Discrete (p_2) motor end plates were found in the interval between the myotube region and the spindle pole. No examples of β innervation were observed in either lumbricals or tongue.

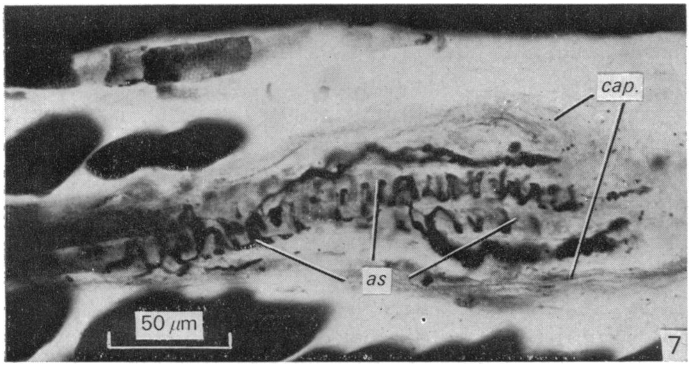
Spiral endings. Three examples were seen of a single, encapsulated muscle fibre supplied by an axon which entered at one pole and formed simple or complex











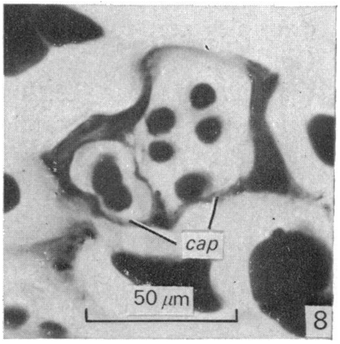


Fig. 3. Muscle spindle from genioglossus of PH10 containing two intrafusal fibres. *cap*, capsule. Gros–Bielschowsky.

Fig. 4. Spindle with five intrafusal fibres in longitudinalis superior of 2DH10. *cap*, capsule; *v*, verticalis. Double impregnation.

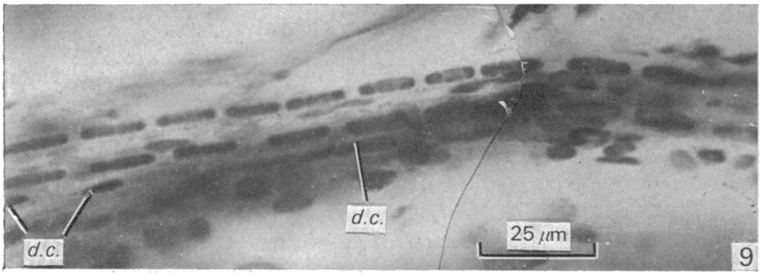
Fig. 5. Spindle from longitudinalis inferior of DH10 containing three intrafusal fibres. *cap*, capsule. Gros–Bielschowsky.

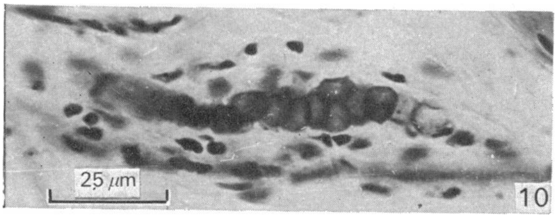
Fig. 6. Chain-like arrangement of nuclei in an extrafusal fibre of CR10. Gros–Bielschowsky.

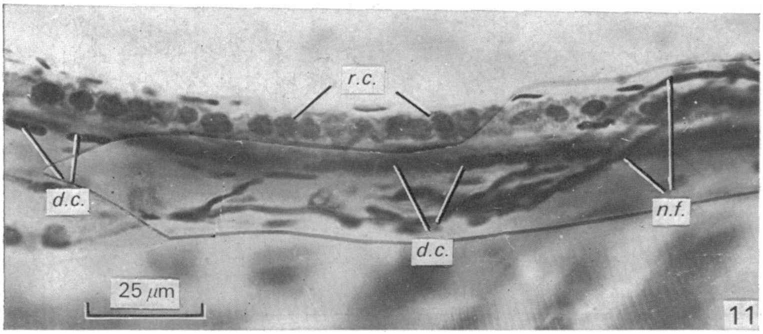
Fig. 7. Spindle in right transversus linguae of DH10. The spindle contained five intrafusal muscle fibres. *as*, annulospiral ending; *cap*, capsule. de Castro.

Fig. 8. Compound spindle (seven intrafusal fibres) from genioglossus of DH10. *cap*, capsule. Gros–Bielschowsky.

spirals along the intracapsular segment of the fibre (Fig. 12). No motor innervation could be detected within the capsule, nor was there a definable equator. In the only example in which the nuclei were stained these formed an oval chain throughout the length of the fibre. These atypical endings bear a close resemblance to the encapsulated spirals described by Sas & Appeltauer (1963) in human extrinsic ocular muscles. One unencapsulated simple spiral was seen (Fig. 14). Simple and







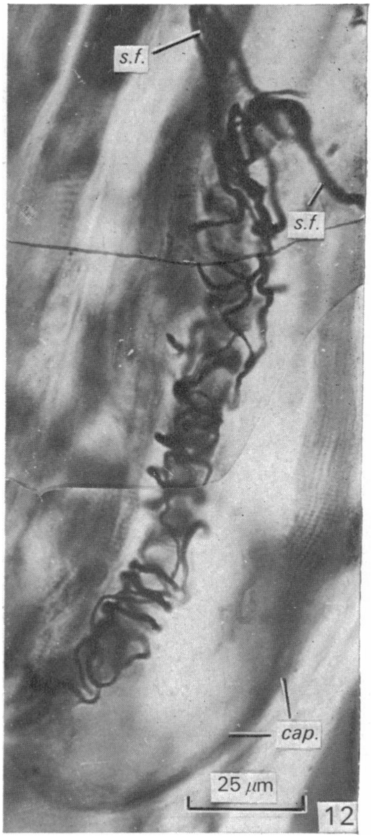


Fig. 9. Dolichonuclear chain (*d.c.*) fibres in denervated spindle in left transversus linguae of DH10. Gros–Bielschowsky.

Fig. 10. Double and single intrafusal nuclei in a denervated spindle in left transversus linguae of DH10. Double impregnation.

Fig. 11. Round-nuclear (*r.c.*) chain in left longitudinalis superior of R14. The spindle also contains dolichonuclear chains (*d.c.*). The nerve fibres (*n.f.*) did not penetrate the capsule and the equator was denervated. Gros–Bielschowsky.

Fig. 12. Complex spiral in right longitudinalis superior of 2DH2. The spirals extended along the entire intracapsular part of the single muscle fibre. *cap*, capsule; *s.f.*, stem fibres. Gros–Bielschowsky.

elaborate unencapsulated spirals were described by Daniel (1946) and Cooper & Daniel (1949) in human extrinsic ocular muscles.

Tendon endings. Tendon endings were found in nine animals (Table 3). All but two were in or near the median septum and were relatively simple in form. A single axon, of 6–8 µm external diameter, branched close to the septum, sometimes having passed through it (Fig. 18). Terminals were formed within the septum or within short lateral extensions of it (Fig. 19). These extensions received individual fibres of the transversus linguae and were therefore microtendons. None of the septal endings was encapsulated.

Two tendon endings were suprahyoid, one near the mid-line in the genioglossus, and the other more laterally in the hypoglossus. The first was large and unencapsulated, some 20 terminals arising from a single parent fibre (Fig. 15). The

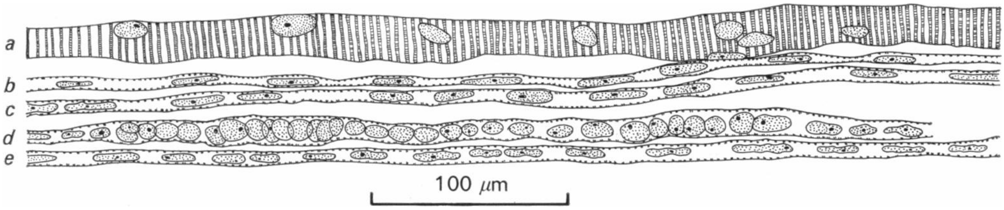


Fig. 13. Tracing of projected muscle fibres and their sarcomeres from left transversus linguae of DH10. *a*, extrafusal fibre; *b*, *c*, *e*, dolichonuclear chain fibres; *d*, round-nuclear chain fibre. The spindle was completely denervated. Gros–Bielschowsky.

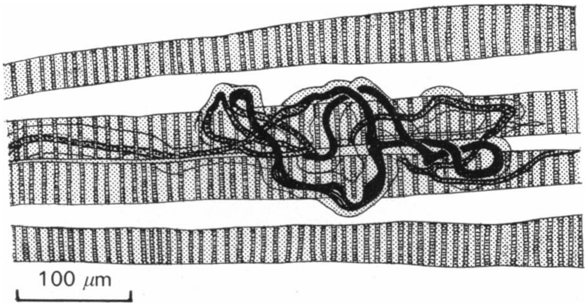


Fig. 14. Traced projection of coiled nerve ending in right transversus linguae of CR14. The lightly drawn parts of the nerve fibre were deep to the muscle fibres. Gros–Bielschowsky.

Table 3. *Normally innervated proprioceptors in the right side, including the mid-line region*

Code	Muscle spindles	Tendon endings	Ruffini endings	Pacinian corpuscles	Paciniform endings	Lamellated endings
L4	12	0	0	0	0	0
L10	+*	8	0	0	0	0
DH2	+	2	0	0	0	0
2DH2	+	0	0	1	0	0
DH10	44	8	12	0	0	0
2DH10	32	4	1	0	1	1
MH2	+	0	0	0	0	2
MH10	+	0	0	2	0	0
PH10	6	0	0	0	0	0
PHL10	+	2	0	1	0	0
C2	+	2	5	1	0	0
C10	7	2	0	2	0	0
R14	28	1	1	0	0	0
CR10	72	0	4	17	0	0
CR14	76	10	29	0	3	1

* + = present but not counted.

second ending had a thick capsule, apparently collagenous, and a cellular core which was permeated by the complex ramifications of one coarse and one fine stem fibre (Fig. 16). The fine fibre presumably represented the accessory innervation found in classical encapsulated tendon organs (Tello, 1922; Weddell & Harpman, 1940; Wohlfart & Hendriksson, 1960).

Ruffini endings. Ruffini endings were found in six animals (Table 3). Six occupied

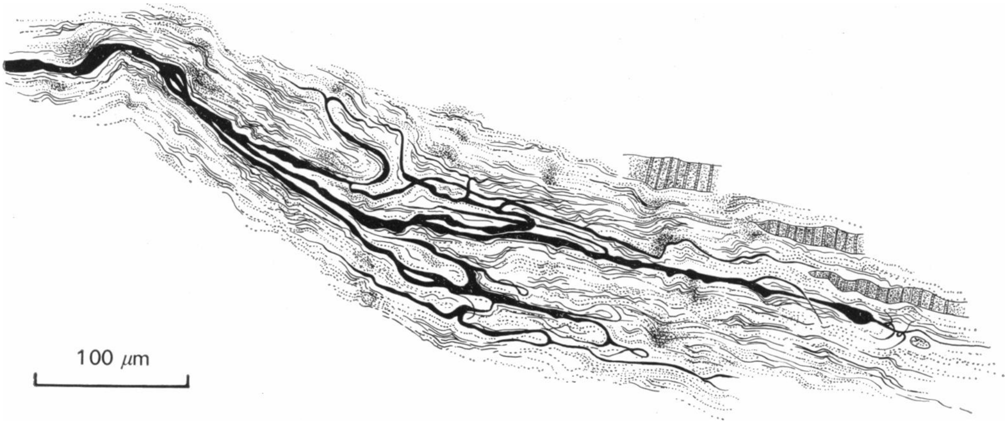


Fig. 15. Traced projection of suprahyoid tendon ending from R14. Gros–Bielschowsky.

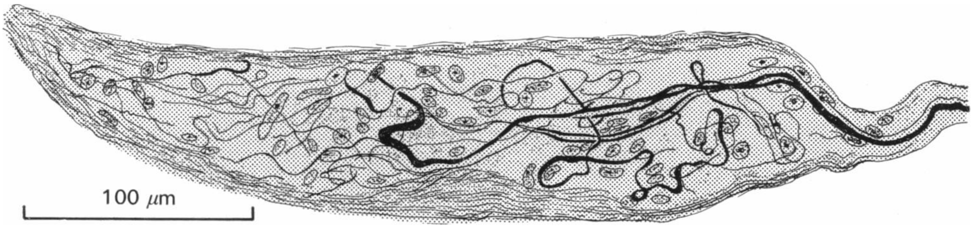


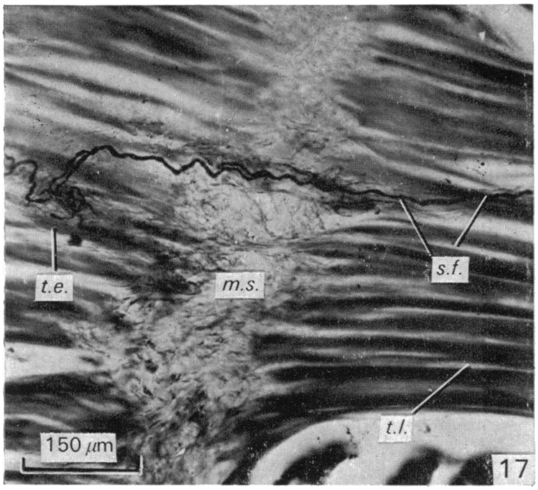
Fig. 16. Encapsulated suprahyoid tendon ending from C2. The stem fibre was accompanied by a fine 'accessory' fibre. Gros–Bielschowsky.

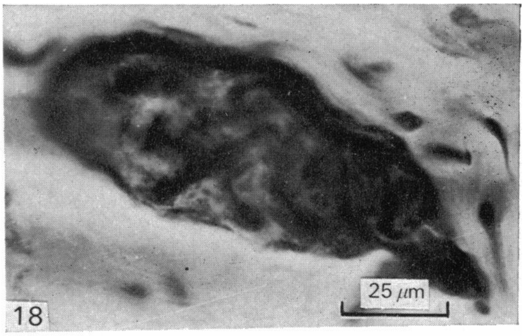
the mid-line fat below the posterior part of the median septum, and the remainder were scattered throughout the musculature. The endings were almost always intermuscular, i.e. they lay in the connective tissue spaces between the various intrinsic and extrinsic muscles. *Typical* forms (Figs. 18, 20–22) resembled the sensory endings described by Andres & von Düring (1973), Andres (1974), and Halata (1977) in skin and around joints. The axon lost its myelin sheath as it penetrated the capsule, and it divided dichotomously. Termination was either by tapering or by the formation of clubs, up to 10 μm thick, embedded in an argyrophilic sheath. Several *atypical* forms were encountered. In some ten instances no capsule could be detected, the ending consisting of a skein of fine interwoven axons (Fig. 23). In four other instances the terminal fibres diverged to create clusters of endings, the parent capsule ensheathing each branch (Figs. 24, 25).

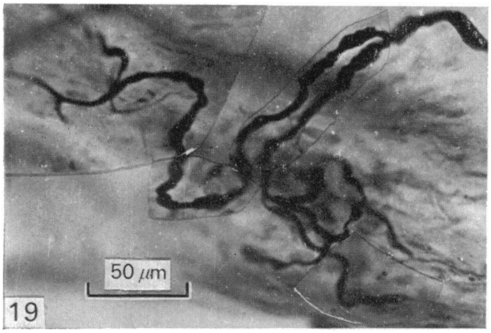
Typical Ruffini endings were numerous in the papillae of the lamina propria of the dorsum of the tongue (Fig. 26).

Pacinian corpuscles. Twenty four innervated Pacinian corpuscles were encountered in six monkeys (Table 3). All were of classical form (Figs. 27, 28, 30), and all but three occupied the mid-line fat below the posterior part of the septum, where they were intimately related to the medial divisions of the hypoglossal nerves. Three were embedded in the medial part of the adjacent genioglossus (Fig. 29).

Paciniform endings. These were rare, only six examples being encountered. They consisted of a straight or J-shaped axon which lost its myelin sheath at the point of entry, and a thin cytoplasmic sheath which could be clearly seen only by reducing







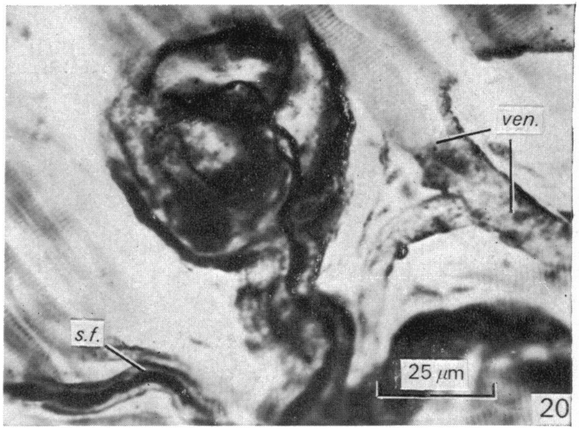


Fig. 17. Tendon ending (*t.e.*) from C2. The stem fibre (*s.f.*) pierced the median septum (*m.s.*). *t.l.*, transversus linguae. Gros–Bielschowsky.

Figs. 18, 20. Ruffini endings from the right side of CR14. *ven*, venule; *s.f.*, stem fibre. Gros–Bielschowsky.

Fig. 19. Enlargement from Fig. 17.

the substage aperture. Like the Ruffini endings, the paciniform endings lay on the surface of extrinsic or intrinsic muscles (Figs. 31, 32).

Lamellated endings. Four were seen. They were distinguished from paciniform endings by their relatively thick sheath. In two, the central axon bifurcated within the proximal core. The smallest measured 120 × 50 μm. The largest (Fig. 33) had a length of 400 μm. Two occupied the mid-line fat, the other two occupied connective tissue spaces within the right genioglossus.

Perivascular endings. In all the material, on both operated and control sides, the lingual artery and its main branches were accompanied by small nerves containing myelinated and unmyelinated fibres. The unmyelinated fibres could be traced onto the surface of the tunica media where they formed undulating bundles suggestive of sympathetic vascular nerves. The destination of all the myelinated fibres could not be determined, but some could be traced to terminals resembling small tendon endings, in the adventitia of primary branches of the lingual artery.

No free nerve endings were found anywhere within the musculature of the tongue.

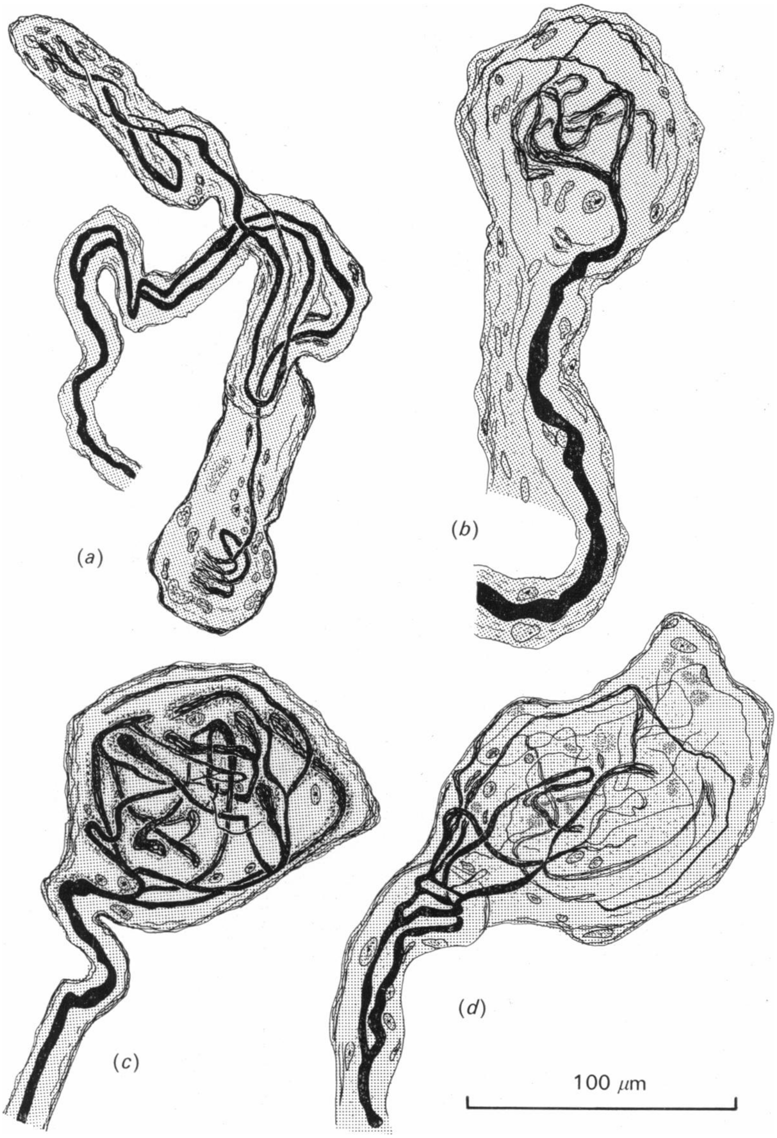
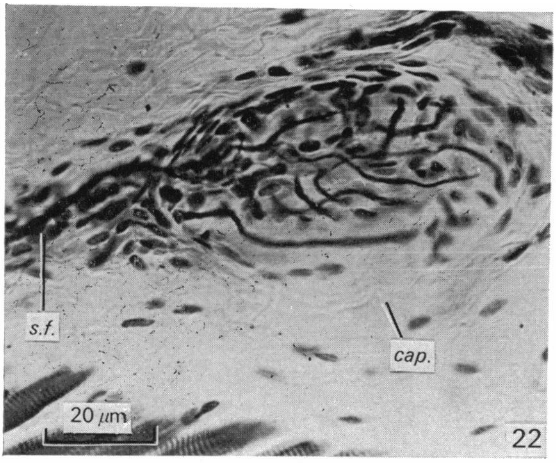


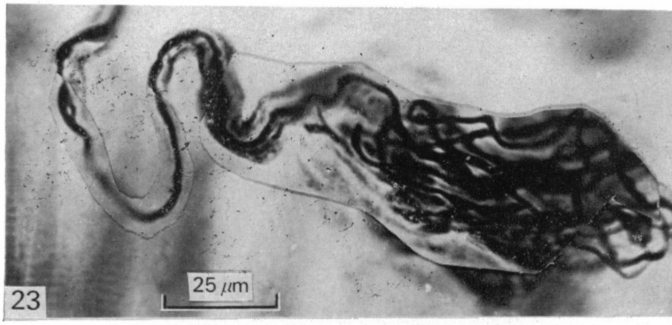
Fig. 21. Traced projections of Gros–Bielschowsky sections showing Ruffini endings on the right side: (*a*) pair from CR10; (*b*) from CR10; (*c*) from DH10; (*d*) from CR14.

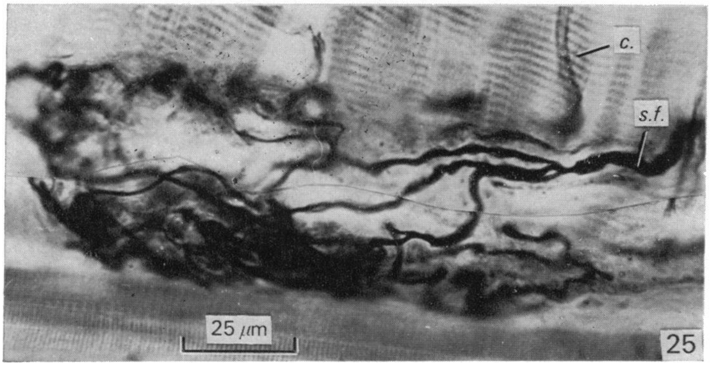
This was surprising, because free nerve endings are numerous in limb muscles (Stacey, 1969).

Experimental findings (Table 4)

Lingual nerve section. After 4 day (L4) and 10 day (L10) survival periods, the histological sections showed degenerating ipsilateral lingual nerve branches on the surface of the hypoglossus, interspersed among normal hypoglossal branches. On post mortem examination, no connexions between lingual and hypoglossal nerves were seen in this region under the operating microscope, in these or any other







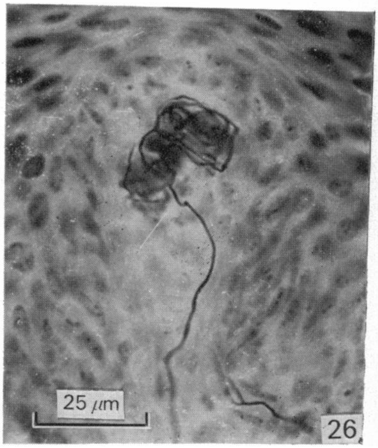


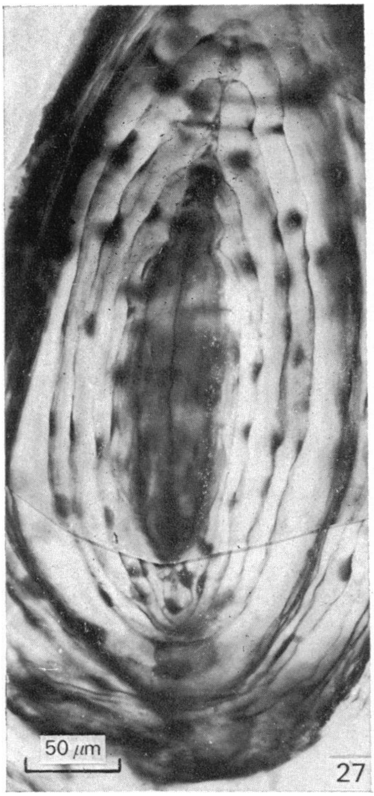
Fig. 22. Ruffini ending from the right side of 2DH10. *cap*, capsule; *s.f.*, stem fibre. Double impregnation.

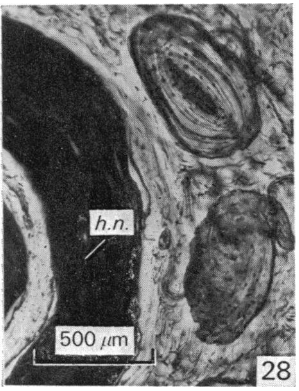
Fig. 23. 'Ball of thread' Ruffini ending (CR14). Gros–Bielschowsky.

Fig. 24. 'Open' type Ruffini ending (CR14) with ill-defined capsule and three stem fibres. Gros–Bielschowsky.

Fig. 25. 'Open' type Ruffini ending (CR14) derived from a single stem fibre (*s.f.*). *c*, capillary. Gros-Bielschowsky.

Fig. 26. Ruffini ending in dorsal mucous membrane of CR10. Gros–Bielschowsky.





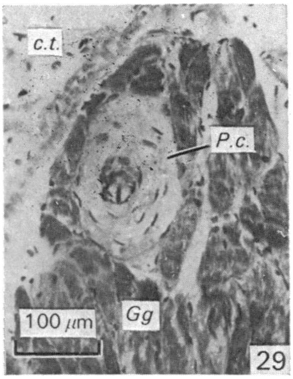


Fig. 27. Pacinian corpuscle from CR10, showing central axon, inner core, outer core, and argyrophilic investing connective tissue sheath. Gros–Bielschowsky.

Fig. 28. Two innervated Pacinian corpuscles beside right hypoglossal nerve (*h.n.*) of CR10. One is enlarged in Fig. 27.

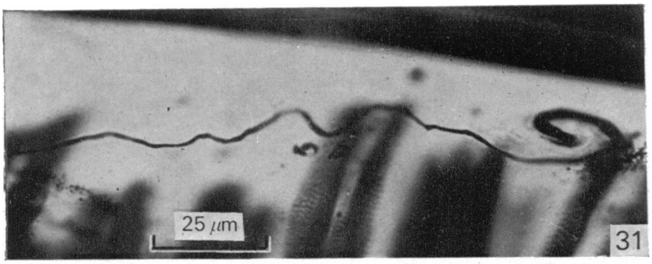
Fig. 29. Pacinian corpuscle (*P.c.*) in the medial part of right genioglossus (*Gg*) of C10. *c.t.*, midline connective tissue. Double impregnation.

Fig. 30. Pacinian corpuscle from CR10. Gros–Bielschowsky.

monkeys. However, at least six lingual–hypoglossal connexions were observed in frozen sections, both in L4 and L10, on or within the genioglossus (Fig. 35). As the lingual nerve branches ascended through the musculature, about 10 % contained a variable proportion of healthy fibres apparently derived from hypoglossal connexions.

Muscle spindles were not visibly affected by cutting the lingual nerve. None of the sections showed degenerating axons within spindle capsules. On the left (operated) side of L2, normal equatorial axons were seen in four of nine spindles and normal polar axons in six. On the right side, normal equatorial axons were seen in seven of twelve spindles and polar axons in six. On both sides the integrity of spindle innervation in oblique sections (usually in genioglossus) was difficult or impossible to ascertain.

In L10, normal equatorial nerve fibres were seen in 21 spindle sections on the left side, and normal polar fibres in 27. (Allowance was not made for repetitive sectioning of spindles.) On the right, normal equatorial fibres were seen in 9 spindle



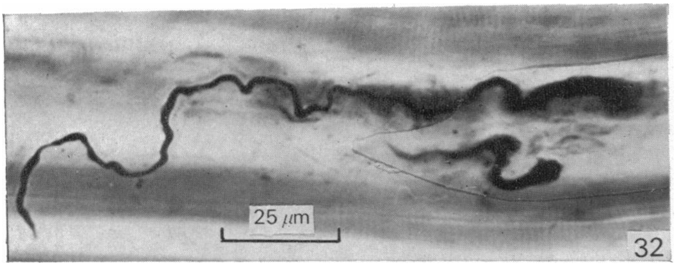


Fig. 31. Paciniform ending from right side of 2DH10. Gros–Bielschowsky.

Fig. 32. Two paciniform endings from right side of CR14. Gros–Bielschowsky.

Fig. 33. Lamellated ending from mid-line connective tissue in MH2. The tip of the axon was bifid (top centre). Gros–Bielschowsky.

sections, and normal polar fibres in 23. Eight separate tendon endings were identified in the median septum. Four parent fibres entered from the left side, three from the right, and in one the side of origin could not be determined. The parent fibres could be followed for distances of 100 μm or less within the transversus linguae.

No degenerating axons were found anywhere in the right side of the tongue in either animal.

Distal hypoglossal nerve section. After 2 days (DH2, 2DH2) the larger ipsilateral hypoglossal branches were filled with myelin ellipsoids and axonal debris. Most of the terminal motor sprays had already disappeared, the remainder being represented by small fragments.

On the left side of DH2, no normal axons were seen in any spindle section. Nerve debris was seen in seven equatorial sections of muscle spindles, and in 16 polar sections. In the anterior quarter nerve bundles could be followed through three separate spindle capsules; in each, all the axons were visibly degenerating (Fig. 34).

Degenerating axons could be traced up to 2 mm into the musculature of the right side in the anterior quarter of the tongue. Conversely, normal axons passed from right to left in the same region, and some of them terminated in motor end plates in the most medial fibres of the left genioglossus. In the right side of the tongue normal axons were seen in 13 equatorial sections of muscle spindles and in 19 polar sections. Two septal tendon endings were found; one parent fibre became lost to view within the septum, and the other was traced for about 100 μm to the right side.

Table 4. *Summary of experimental findings*

	Muscle spindles		
Nerve section (and code)	Equators	Poles	Other proprioceptors
(*a*) Lingual (L)	Unaffected	Unaffected	None seen
(*b*) Distal hypoglossal (DH)	Denervated*	Denervated	Denervated
(*c*) Mid-hypoglossal (MH)	Some denervated	Denervated	Uncertain
(*d*) Proximal hypoglossal (PH)	Unaffected	Denervated	None seen
(*e*) (*a*)+(*d*) (PHL)	Unaffected	Denervated	Uncertain
(*f*) C2–C3 connexion (C)	Some denervated	Unaffected	Some denervated
(*g*) Ramus descendens (R)	Unaffected?	Unaffected	Uncertain
(*h*) (*f*)+(*g*) (CR)	Denervated*	Unaffected	Denervated*

* Some residual innervation, ? from transmedian overlap.

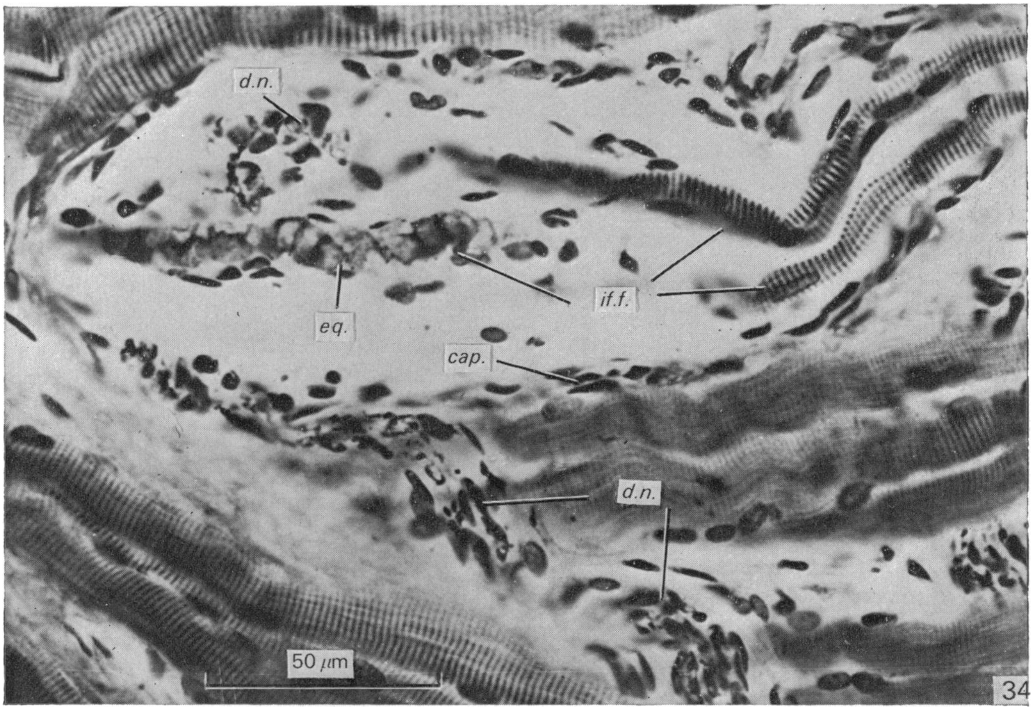


Fig. 34. Spindle from left side of DH2. Degenerating nerve bundle (*d.n.*) pierces the capsule (*cap.*) from below. Further degenerating nerve fibres occupy the lymph space. *eq.*, denervated equator containing round nuclei. *if.f.*, intrafusal muscle fibres. Double impregnation.

In the second animal (2DH2) autopsy showed that section of the hypoglossal nerve was not quite complete. Several fine filaments left the upper border of the trunk immediately proximal to the site of section; the filaments interdigitated with lingual nerve branches and entered the posterior part of the hypoglossus. Stained sections showed several normal motor end sprays in this region of hypoglossus and in the underlying portion of genioglossus. The same sections showed intact annulospiral endings in one hypoglossal spindle and in two genioglossal spindles in this region. No other innervated spindles were found on the left side. Two small

Pacinian corpuscles were found in the mid-line. One contained a normal axon, the other was too densely stained to permit study of its core.

After 10 days (DH10, 2DH10) the left hypoglossal nerve had undergone extensive degeneration. In both animals several communications with the healthy lingual nerve were observed. The smallest visible branches of the degenerated hypoglossal, consisting of empty neurolemmal sheaths, were about 15 μm thick, the terminal motor sprays having disappeared without trace. However, normal motor sprays were seen in DH10 in one fascicle of verticalis immediately to the left of the median septum, and the parent nerve bundle was seen to penetrate the septum from the right side.

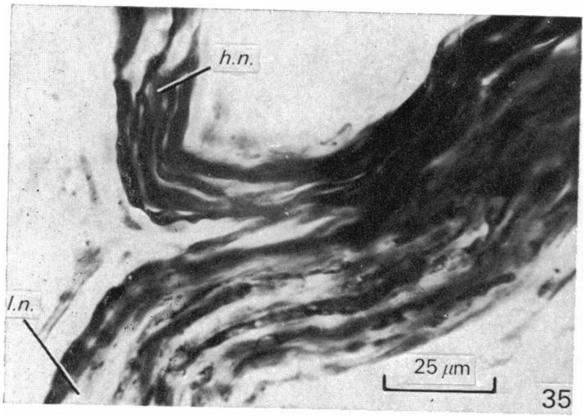
In the left half of DH10, 20 separate spindles were identified. In 18 of these no healthy nerve fibres were found (Figs. 9, 10, 13); the entering nerves were represented by empty neurolemmal sheaths which could be followed for short distances within the capsules. In the remaining two, apparently healthy axons were found within the capsule close to intrafusal muscle fibre equators. Both spindles were in the anterior quarter of the tongue, about 2 mm from the mid-line. The right side of DH10 showed 44 spindles, 10 in intrinsic and 34 in extrinsic muscles. All contained only healthy intracapsular axons.

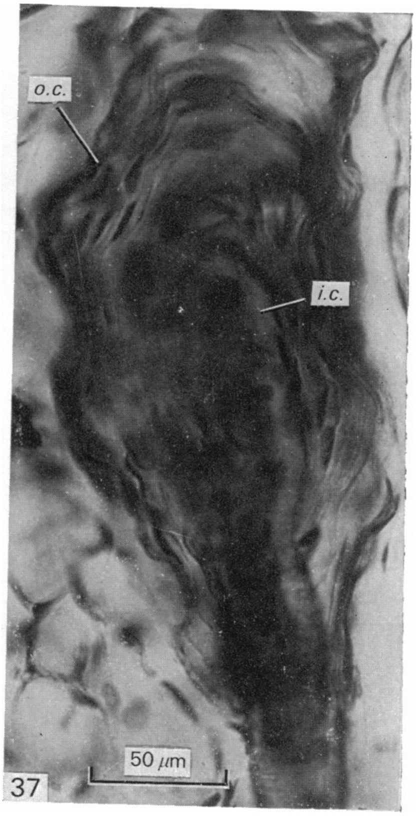
In 2DH10 the cervical–hypoglossal connexion was found at autopsy to be anomalous. On both sides, the common stem formed by C2–C3 entered the upper end of ramus descendens hypoglossi instead of entering the hypoglossal nerve directly. In the left half of the tongue, 16 muscle spindles were observed in intrinsic muscles, and six in extrinsic muscles. Seventeen of these were denervated. The other five showed normal equatorial innervation; whether they had intact polar nerves was not clearly established. One of the five was in the most medial part of genioglossus; the others were in longitudinalis superior – surprisingly, nearer to the lateral margin than to the mid-line. In the right half of 2DH10, 32 spindles were observed, all with normal innervation.

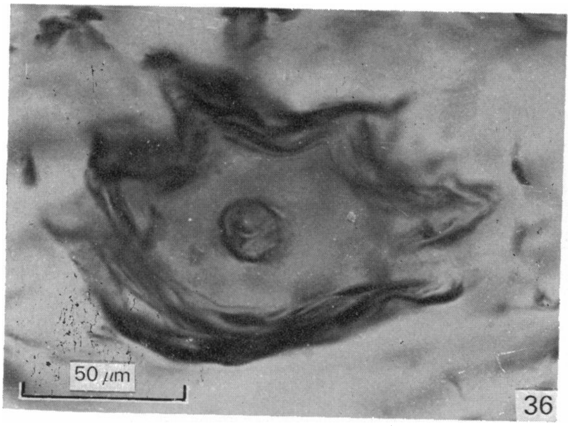
Tendon endings were observed in the median septum, eight in DH10, four in 2DH10; the parent fibre entered from the right in all twelve. Twelve Ruffini endings were found in DH10, all on the right side, scattered through the anterior three quarters of the tongue. In 2DH10 a single Ruffini ending was found on the right side (Fig. 22).

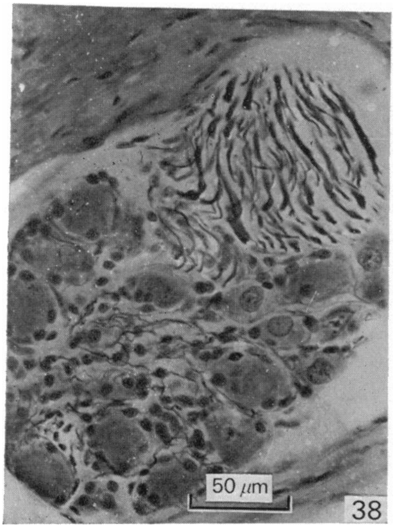
Section of mid-hypoglossal nerve. After 2 days (MH2) the ipsilateral hypoglossal nerve branches (including the primary branches) contained globular debris and irregular axonal segments, together with small numbers of apparently healthy myelinated and unmyelinated nerve fibres. On the left side the equatorial regions of six separate spindles were clearly displayed in longitudinal section. In four of these the primary afferents appeared normal; one also showed an intact secondary afferent. In two of the four the parent afferent fibres could be traced proximally through the capsules to their points of emergence from otherwise degenerate hypoglossal bundles. The polar regions of all four contained axonal debris, with no intact nerve fibres. On the right side, normal equatorial innervation was observed in ten separate spindles and normal polar innervation in eight.

After 10 days (MH10) the main hypoglossal branches were largely clear of debris. They contained scattered intact nerve fibres. On the left side, normal equatorial fibres were seen in five sections of spindles; no polar axons were seen. On the right, normal equatorial innervation was seen in twelve spindle sections and normal polar innervation in three. Two normally innervated Pacinian corpuscles, each









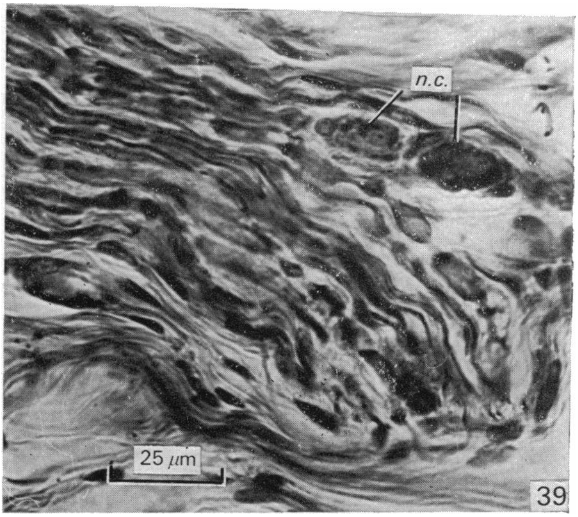


Fig. 35. Junction of degenerating lingual (*l.n.*) and hypoglossal (*h.n.*) nerve branches on the left side of L4. Gros–Bielschowsky.

Fig. 36. Transverse section of denervated Pacinian corpuscle adjacent to left hypoglossal nerve of CR10. The outer core lamellae have collapsed. Gros–Bielschowsky.

Fig. 37. Longitudinal section of denervated Pacinian corpuscle adjacent to left hypoglossal nerve of CR10. The nerveless inner core (*i.c.*) appears relatively normal, but the outer core (*o.c.*) has collapsed. Gros–Bielschowsky.

Fig. 38. Ganglion on branch of right lingual nerve of L10. Double impregnation.

Fig. 39. Nerve cells (*n.c.*) in a degenerating nerve on the left side of 2DH2. Double impregnation.

about 200 μm in diameter, were found in the mid-line fat in MH10. One was supplied from the medial division of the right hypoglossal nerve, the other by one of several healthy 50 μm diameter nerve bundles which lay adjacent to the degenerated medial division of the left hypoglossal.

Hypoglossal nerve section at base of skull. In the single case in which hypoglossal section alone was attempted at the base of the skull (PH10), histological sections indicated that the neurotomy had been incomplete. In the anterior part of the tongue at least half the motor end sprays were intact on the left side, and they could be traced back to normal fibres in primary branches of the left hypoglossal nerve. This tongue appeared to be devoid of any proprioceptors other than muscle spindles: seven were seen on the left side and six on the right. In two spindles on the left, axonal debris was observed in the polar regions; both had intact equatorial nerve fibres.

In PHL10 the connective tissue spaces were permeated by bundles of degenerate lingual and hypoglossal fibres. Degeneration was total in the major branches of the lingual nerve, but the hypoglossal branches contained numerous intact fibres. On the left side thirteen normally innervated equatorial sections of spindles were encountered, and four on the right side. No section showed evidence of equatorial denervation. Polar innervation was not satisfactorily demonstrated in sections from either side. Two septal tendon endings were observed, the parent fibre of one approaching from the left, that of the other being lost to view in the septal connective tissue. A single Ruffini ending was found on the left side, 0·5 mm from the mid-line; its axon was traced to the septum, but its side of origin could not be demonstrated. A single Pacinian corpuscle, 200 × 130 μm, was found in the mid-line fat; its axon was intact and could be traced into a largely degenerate hypoglossal bundle on the left side.

Section of the C2–C3 connexion. After 2 days (C2), degenerating fibres were scattered among branches of the left hypoglossal nerve throughout the tongue. Four spindle sections on the left contained normal equatorial nerve endings and ten contained normal polar endings. Eleven sections showed intracapsular axonal debris at the level of spindle equators. On the right side, 20 spindle sections contained normal equatorial endings and 14 contained normal polar endings. Two tendon endings were seen, one beside the median septum (Fig. 17), and one suprahyoid (Fig. 16). Eight normally innervated Ruffini endings were observed, one in the mid-line, three on the left side and four on the right. One innervated and two denervated Pacinian corpuscles were seen in the mid-line fat.

After 10 days (C10), degenerated axonal remnants were found only occasionally in ipsilateral hypoglossal nerve bundles. Only 14 separate spindles could be identified, seven on each side. In none was equatorial innervation satisfactorily demonstrated. On the left side, normal polar nerve fibres were seen in six sections (three spindles). Two small tendon endings were found in the median septum, both supplied from the right side, and two innervated Pacinian corpuscles occupied the mid-line fat.

Section of ramus descendens of the hypoglossal nerve. Examination of the osmium-stained ramus descendens of the right side showed it to consist of two nerve bundles which diverged as they entered the Y-junction with the hypoglossal trunk. Above the level of nerve section on the left the posterior bundle appeared normal; the anterior bundle had degenerated, its fibrous remnant entering the hypoglossal nerve as the anterior, shrunken limb of the Y. Below the level of section the appearances were reversed, the anterior bundle being normal whereas the posterior one had degenerated. These findings indicated that the ramus descendens had two components, a descending (posterior) bundle presumably for distribution via the ansa cervicalis, and an ascending bundle which entered the hypoglossal proximal to the origin of the branches to geniohyoid and thyrohyoid.

On the left side of the tongue, 32 sections of spindle equators displayed normal innervation in 26. The other six equators appeared to be devoid of nerve fibres (Fig. 11), all six being close to the inferior surface of the tongue. On the right side, 28 spindles were encountered, all with well-defined annulospiral endings. Thirty three examples of polar innervation were identified. A single tendon organ was found in the mid-line in the suprahyoid region, and a single Ruffini ending was found on the right genioglossus.

Section of C2–C3 connexion and ramus descendens hypoglossi. At 10 days (CR10), the branches of the left hypoglossal nerve were infiltrated with nerve fragments in an advanced state of degeneration. No instance of normal equatorial innervation was found in 28 spindles here, or in four located in mid-line fibres of genioglossus, but ten spindle sections showed normal polar fibres. The right side contained 72 spindles, equatorial innervation being detectable in 25 sections and polar innervation in 14. Four Ruffini endings were found on the right side, none on the left. Pacinian corpuscles were observed in 61 sections, and reconstructions showed their total to be 25. Seventeen were normally innervated, four of these lying on the medial division of the right hypoglossal and 13 in the adjacent fat. Eight were denervated. They also occupied the mid-line fat but they were, in general, closer to the left hypoglossal than to the right (Fig. 40). The denervated corpuscles had a collapsed appearance created by irregular shrinkage of the interlamellar spaces (Figs. 36, 37). This change was more pronounced than is usual in experimentally denervated corpuscles (Chouchkov, 1971; Wong & Kanagasuntheram, 1971; Krishnamurti, Kanagusuntheram & Vij, 1973).

After 14 days (CR14) axonal remnants could still be detected in some of the larger hypoglossal branches on the left side, but degenerated fibres were difficult to find elsewhere. The tongue of this animal was the richest in proprioceptors. Some 300 spindle sections were encountered. Reconstruction of the entire tongue gave a count of 132 spindles (Table 5). On the left side, three spindles had retained their annulospiral endings. One of the three occupied longitudinalis inferior, 0·7 mm to the left of the mid-line, where there was a side-to-side continuity of intrinsic muscles below the median septum. The other two were within 3 mm of the tip of the tongue, in transversus linguae. Forty nine sections of normally innervated spindle poles were observed. On the right side, annulospiral endings were seen in 43 spindle sections, and polar innervation in 49 sections. Ten tendon endings were found in the median septum. In five the axons entered from the right, in three from the left, and in two the axons were lost to view within the septum. The tendon endings were all located 0·5–3 mm from the tip of the tongue.

On the left side, 14 Ruffini endings were found, all within 4 mm of the tip of the tongue, and eight within 2 mm of the mid-line. Two were close to a motor band in transversus linguae; in both, the parent fibre emerged from a bundle which gave rise to an adjacent spray of motor end plates. Two others were atypical, being embedded within transversus linguae. On the right side five Ruffini endings were seen in the middle third of the tongue, and 24 others within 4 mm of the tip. Three paciniform endings were seen on the right side, none on the left.

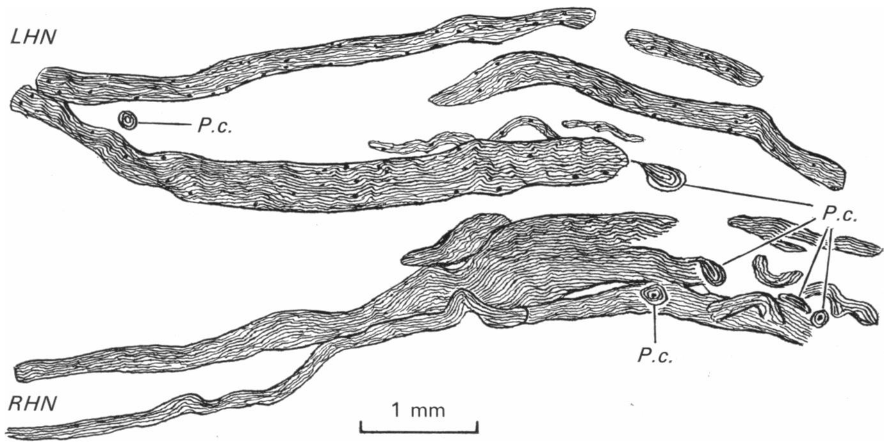


Fig. 40. Graphic reconstruction of the mid-line region of CR10. The left hypoglossal nerve (*LHN*) contained scattered nerve debris (represented by dots). The two Pacinian corpuscles related to LHN were denervated. The four corpuscles related to the right hypoglossal (*RHN*) were innervated. Eight Gros–Bielschowsky sections.

Table 5. *Distribution of muscle spindles in monkey CR14*

Muscle	Left	Right	Total
Verticalis	8	27	115
Transversus	25	32	
Longitudinalis	14	9	
Genioglossus	5	4	17
Hyoglossus	2	1	
Styloglossus	2	3	
Total	56	76	132

Note on intralingual ganglia

Nerve cell bodies were found, singly or in groups, on branches of the glossopharyngeal, lingual, and hypoglossal nerves. Structurally, the glossopharyngeal and lingual ganglia were indistinguishable, and both were numerous in the region of the intralingual salivary glands. Typically, the nerve cells formed spherical clusters which appeared as rosettes in section, the centre of each being occupied by a web of fine, unmyelinated axons which escaped to rejoin the related nerve bundle. Although the ganglia were considered to be autonomic, the small size of the nerve cell bodies (10–20 μm diameter), and their investment of satellite cells, made it impossible to distinguish axons and dendrites. Occasional cell bodies showed a surface 'dust' suggestive of boutons terminaux.

Ganglia of autonomic type were not restricted to the territory of the minor salivary glands. Nerve cell bodies were scattered singly or in groups of two to 20 on nerve branches in the musculature throughout the entire tongue (Fig. 38). The degeneration studies made it abundantly clear that these cell bodies belonged, in roughly equal numbers, to branches of both the lingual and hypoglossal nerves. The only distinction that could be drawn between lingual and hypoglossal cell bodies was the greater tendency of those on the hypoglossal to be found singly or in short chains (Fig. 39).

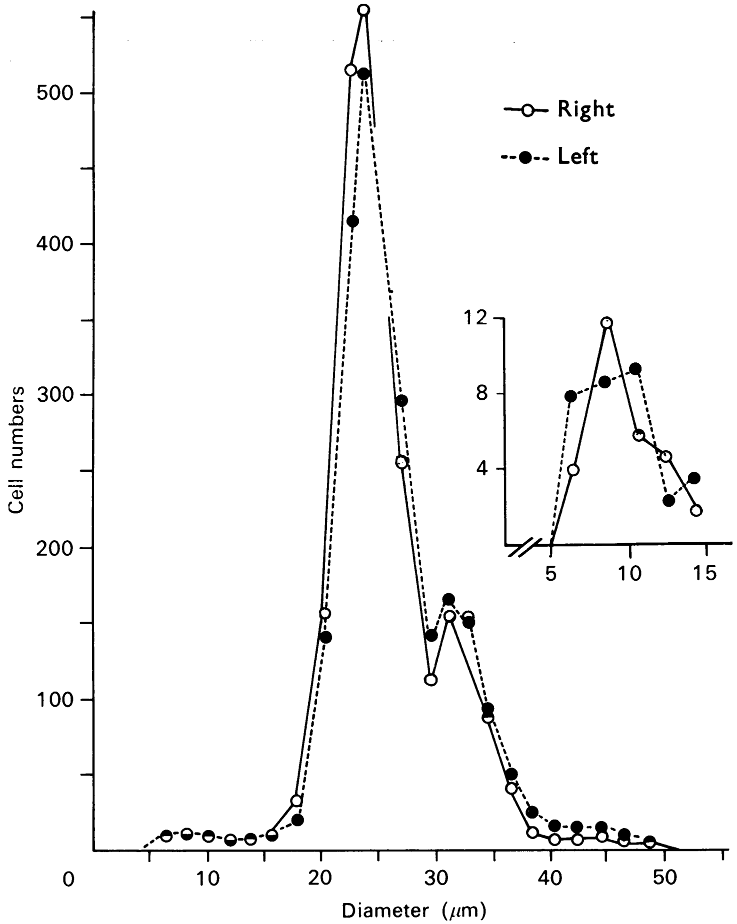


Fig. 41. Mean cell diameters (from maxima and minima of cells displaying nucleoli) in the hypoglossal nucleus of DH10. The left part of the Figure is enlarged in the inset.

The destination of the unmyelinated fibres emerging from these intramuscular ganglia was not determined. They rejoined the parent nerve branches and proceeded distally within them. There was no consistent contiguity between the ganglia and the small arteries permeating the musculature.

The hypoglossal nucleus

The present observations were confined to a search for fusimotor neurons within the nucleus. In the spinal cord (cat) fusimotor neurons are adjacent to the alpha motor neurons in the ventral horn and are about one third as large. Unlike interneurons, they exhibit chromatolysis following section of appropriate ventral nerve roots (Nyberg-Hansen, 1965).

The mean diameters of hypoglossal neurons showed a large peak at 20–26 μm and a smaller peak at 30–34 μm (Fig. 41). Whether this represented a bimodal distribution of cell size, or merely of cell orientation, was not determined. In the range of 6–9 μm about 20 nerve cells were found within the medial part of each nucleus at the level of the inferior limit of the fourth ventricle. The nuclear diameter of these cells was about one third of those whose measurements exceeded 10 μm. Ten days after peripheral hypoglossal nerve section chromatolysis was not convincingly displayed by these small cells. On the right (control) side Nissl material was diffuse rather than discrete, and was peripheral rather than central. On the left the appearances were much the same. In the larger cells throughout the left nucleus, however, dispersal of Nissl substance was obvious, although the mean cell size increased by only 1 % (from 26·42 μm on the right to 26·65 μm on the left in DH10).

A second small-cell group (mean diameter 7 μm) was observed immediately lateral to the rostral part of the hypoglossal nucleus. This was considered to be the nucleus intercalatus of Staderini (1895).

No sensory type neurons were observed in relation to the intramedullary fibres of the hypoglossal nerve.

The mesencephalic nucleus

This round-celled nucleus extended, ribbon-like, from upper pons into mid-brain beside the cerebral aqueduct. On each side, 1–2 % of cells showed dispersal of Nissl substance, a feature noted by other workers. Following cervical nerve section the appearances were not appreciably altered. The somatotopic organization of the mesencephalic nucleus is diffuse rather than localized, at least in relation to input from the masticatory muscles (Corbin & Harrison, 1940; Jerge, 1963), which are represented bilaterally (Smith, Marcarian & Niemer, 1968).

DISCUSSION

The proprioceptive innervation of the Cynamolgus monkey tongue is remarkable both for its range of structural forms and for its quantitative variability. The only proprioceptor constantly present is the muscle spindle. Spindle counts of eight whole tongues ranged from 13 to 132, and no meaningful relationship appeared to exist between the numbers of spindles and of other proprioceptors. There was no indication of an inverse proportion between the sums of spindles and of other receptors. In two extreme examples the opposite was true: the tongue with fewest spindles showed no other proprioceptors, and that with the largest number of spindles had the largest number of Ruffini endings. Technical procedures could account for small variations between one tongue and another, notably in the anterior and posterior quarters of the tongue where three different techniques were used, but they could not explain the wide spectrum of findings from the middle half, where the same technique was used throughout. The inference that the major variations were genuine was strengthened by the absence of Pacinian corpuscles from nine animals: had they been present they would have been revealed by even the crudest technique. Such variation is explicable on the basis of phylogenetic emergence, for it is a feature of emergent characters generally (Ashton, personal communication). In this connexion it is pertinent that the primates appear to be the first mammalian order in which the tongue acquires the full range of proprioceptors.

Muscle spindles

Classical nuclear bag fibres are remarkably rare in the Cynamolgus monkey tongue, although they are common in the lumbrical muscles. Intermediate fibres are also rare. Chain fibres with spherical nuclei are relatively common, and dolichonuclear chains have been found in every spindle. The traditional classification of intrafusal fibres into bag and chain types does not hold good for the Cynamolgus monkey tongue. A comparable arrangement of intrafusal fibres has been observed by Banks & James (1973) in the lumbrical spindles of the guinea-pig, in which the equators are only about 150 μm long. In those spindles the widest fibres were of intermediate type, the remainder being nuclear chains. The chain nuclei were all cylindrical, but the sarcoplasmic fine structure of the chain fibres permitted recognition of two types of chain; a total of three intrafusal fibre types was therefore defined. The existence of three distinct types of intrafusal fibres, at least in rat, rabbit, guinea-pig, cat and man is now beyond dispute (Banks, 1971; James, 1971; Maynard & Tipton, 1971; Milburn, 1973; Boyd, 1977; Banks, Harker & Stacey, 1977; Barker *et al.* 1977; Boyd, Gladden, McWilliam & Ward, 1977). The evidence is histochemical, ultrastructural, and electrophysiological. Silver staining alone is insufficient to distinguish the three types with confidence. In most species there are two nuclear bag fibres, the 'bag_2' fibre being slightly larger than the 'bag_1'; the standard chain fibre is the third. In the guinea-pig lumbrical the intermediate fibre corresponds to the 'bag_2', and the 'bag_1' forms two types of chain. In the monkey tongue the bag and intermediate forms may be tentatively assigned to the bag_2 group, the round-nuclear chains to the 'bag_1', and the dolichonuclear chains to the third group.

Other proprioceptors

The tendon endings in the median septum were devoid of any apparent capsule, as was a single large example in the suprahyoid region. Dogiel (1902, 1903) described similar non-encapsulated endings in the intramuscular connective tissue of the body wall of various mammals, but he did not observe them in tendons. Classical Golgi tendon organs are encapsulated and contain a much greater profusion of nerve terminals (Schoultz & Swett, 1974; Bannister, 1976). Nevertheless, it is reasonable to consider that the observed tendon endings in the tongue function as tension recorders, septal endings being activated by transversus linguae, and suprahyoid endings by protraction of the tongue. Golgi tendon organs, at least, are highly sensitive to active stretch, responding even to the contraction of single muscle fibres (Jansen & Rudjford, 1964; Alnaes, 1967; Houk & Henneman, 1967).

Ruffini endings, Pacinian and paciniform corpuscles, and lamellated endings are known to occur on the surfaces of muscles and tendons, and in relation to joint capsules (Stilwell, 1957*a*, *b*; Barker, 1962, 1974; Poláček, 1966; Matthews, 1972; Peters, Winkelmann & Coventry, 1972). Their discovery within the tongue was surprising at first, but topologically they are intermuscular here as elsewhere: the tongue is an ordered assembly of individual muscles, the receptors lying in the intervals between them.

The function of the total array of lingual proprioceptors in the monkey is a matter for speculation, particularly in the context of kinaesthesia. Conscious position sense of the tongue and of the eye (Skanevski, 1972) is achievable without movement at a joint. Traditionally, position sense in the limbs has been attributed primarily to the activity of articular receptors, muscle spindles being regarded as concerned in the control of posture and movement and not in perception (Werner & Whitsel, 1973). The Ruffini endings of joints are highly sensitive and slowly-adapting, signalling the speed and direction of small movements (Eklund & Skoglund, 1960). Pacinian, paciniform and lamellated endings are rapidly adapting and respond transiently to movement in any direction, their frequency of response being a function of the speed of movement (Burgess & Clark, 1969; Skoglund, 1973). Joint receptors relay to the postcentral gyrus, where individual cells respond to a given joint position by steady state discharge. Joint movement (in monkeys) increases the discharge rate of some of the cortical cells and reduces the rate in others immediately adjacent (Mountcastle, 1957; Mountcastle & Powell, 1959). By extrapolation, the morphologically similar proprioceptors in the tongue could be considered to provide the substrate for perception of position and movement, the requisite stimulus presumably being the compression exerted by contraction of adjacent muscle groups.

Recent evidence, while acknowledging the contribution of joint receptors, implicates muscle afferents also, certainly in man. Perceived sensation from muscles may be derived from spindles (Goodwin, McCloskey & Matthews, 1972; McCloskey, 1973; Matthews, 1977), but the evidence is still circumstantial (Gandevia & McCloskey, 1976).

The source of proprioceptors

It is now beyond doubt that the hypoglossal nerve is the main portal of exit of proprioceptor fibres from the monkey tongue. Section of the hypoglossal just proximal to its lingual branches produced ipsilateral degeneration of most or all of the intramuscular and intermuscular sensory terminals, whereas lingual nerve section had no apparent affect on them. It is reasonable to conclude also that these afferents leave the hypoglossal to enter the spinal cord via the cervical spinal nerves, the evidence being that destruction of the cervical nerve connexions to the hypoglossal caused virtually complete depletion of ipsilateral proprioceptor endings whereas hypoglossal section at the skull base did not produce detectable sensory fibre loss. All these results are consistent with the neurophysiological observations of Bowman & Combs, which suggested a hypoglossal–cervical route for muscle spindle afferents in the rhesus monkey. The present findings indicate that other proprioceptors also use this route.

The significance of the Y-junction between the ramus descendens and the twelfth nerve was appreciated quite late in the present study, following the preservation of some proprioceptors when the C2–C3 connexion was severed, or when the hypoglossal was sectioned between this connexion and the Y-junction, and their almost complete elimination when the section was distal to the Y-junction, or when both the upper and the lower cervical–hypoglossal connexions were cut. The proximal limb of the Y contains descending axons (as is well known) and the distal limb contains ascending axons. An unknown proportion of the distal limb axons may have been motor (to geniohyoid and thyrohyoid). It could be concluded, at least, that the ramus descendens was a significant afferent pathway from the tongue to the spinal cord. That it might function in this connexion was implied by Corbin, Lhamon & Petit (1937) and by Corbin & Harrison (1939). Moreover, Pearson (1939) observed the same Y-shaped connexion in human embryos, as did Van der Sprenkel (1924) in the hedgehog; and Pearson pointed out that the connexion is initially almost horizontal, the angulation being introduced by the descent of the ansa cervicalis.

The lingual–hypoglossal linkages within the tongue may be viewed as an economical transport system. Just as the cervical nerves utilize the terminal hypoglossal for transport of lingual afferents, adjacent lingual and hypoglossal branches may share a common epineurial sheath for some distance without any functional connexion being implicit in this arrangement. The observed presence of extrafusal motor axons in the linkages in the tongue supports the view that, where they exist, they are merely common pathways for all forms of motor and sensory fibres. In an earlier study on the pig (FitzGerald & Law, 1958), it was concluded that the lingual nerve supplied proprioceptors by means of this pathway, but the observed nerve endings in the connective tissue of the pig's tongue were ill-defined, and the possible access to the tongue of afferent fibres via the ramus descendens hypoglossi was not taken into account.

On phylogenetic grounds, a cervical nerve contribution to the tongue is entirely in accord with expectation. The lingual and infrahyoid muscles of tetrapods constitute the hypobranchial muscle sheet which is derived from occipital and upper cervical somites and extends forwards below the gill arches (Parker & Haswell, 1962). The muscle sheet is supplied by the spino-occipital nerves, of which the hypoglossal is the highest member. The hypoglossal innervates the fused occipital myotomes and represents several fused spinal nerves which have lost their dorsal nerve roots (Romer, 1970). In amphibians the hypoglossal nucleus occupies the upper part of the spinal cord, and its rootlets merge with those of C2 spinal nerve (Kappers, Huber & Crosby, 1967). In higher vertebrates the nucleus has shifted dorsofrontally to occupy the medulla oblongata (Papez, 1967), but in some mammals its dorsal part continues to contribute to the supply of the infrahyoid muscles via the ramus descendens (Lewis, Flumerfelt & Shute, 1971). In this light, the cervical sensory supply to the primate tongue is indicative of a rostral extension of the sensory territory of the more caudal cervical nerves to 'compensate' for the missing hypoglossal dorsal roots.

Acceptance of the hypoglossal–cervical route for lingual afferents is insufficient to account for the present post-operative findings unless some sensory overlap across the mid-line is conceded, especially near the tip of the tongue. In this region CR14 showed persistent ipsilateral equatorial innervation in two spindles, also persistent Ruffini endings; DH10 showed two normally innervated spindle equators, and 2DH10 showed five. The existence of transmedian vascular anastomosis in the anterior part of the mammalian tongue is well known, and the observed passage of nerves across the mid-line below the anterior part of the median septum in the present material provides a plausible basis of explanation for the anomalous persistent innervation. There is indirect evidence for sensory overlap in soft tissues in the anterior part of the mouth, at least in man (Rood, 1977). The observed motor overlap to extrafusal muscle fibres was less extensive than that previously found in the cat (Alexander & FitzGerald, 1968).

The location of the cell bodies of the proprioceptor neurons is not certain. It is remotely possible that they are within the mesencephalic neurons of the trigeminal nerve, although this would presumably require uninterrupted passage of the peripheral cell processes from the tongue through the spinal cord and brain stem. The second and third cervical dorsal roots are more probable (a ganglion is usually absent from Cl spinal nerve in the monkey). Each of these ganglia contains about 5000 nerve cells, about 1 % showing the appearances of chromatolysis in control material (FitzGerald & Sachithanandan, unpublished observations). It seems at present that the location of the relevant cell bodies can only be determined by physiological methods.

Fusimotor nerves evidently accompany the twelfth nerve throughout its course. Polar innervation of muscle spindles was eliminated by section of the nerve at high, middle or low levels, and it was preserved following removal of the cervical nerve connexions. The small-celled group in the medial part of the hypoglossal nucleus may be provisionally designated as the nucleus of origin of the fusimotor neurons. The cell numbers appear to be sufficient for this role; in cat lumbrical muscles, at least, individual stem fibres supply about nine intrafusal muscle fibre poles located in up to five separate spindles (Adal & Barker, 1965). Schwentker (1927) observed a group of small cells in a comparable location in the hypoglossal nucleus of man.

The intralingual ganglia

Ganglia of autonomic type have been seen by others on both lingual and hypoglossal nerve branches within the tongue in man (Sakla, 1964) and rat (Chang, Wang & Lu, 1966). Degeneration experiments in cats (FitzGerald & Alexander, 1969) showed abundant ganglia on lingual nerve branches, but none on the hypoglossal. In the cat the minor salivary glands are restricted to the posterior part of the tongue, and the more anterior ganglia, which are cholinesterase-reactive, were tentatively considered to contain parasympathetic vasodilator neurons. In the present work no histochemical study was undertaken and it could only be surmised that the hypoglossal-related ganglia were autonomic.

SUMMARY

The proprioceptive innervation of the tongue has been investigated in the Cynamolgus monkey by silver impregnation methods following unilateral section of lingual, hypoglossal, and cervical nerves.

Muscle spindles were constantly present in the intrinsic and extrinsic muscles. They varied greatly in number, averaged half the length of lumbrical spindles, and showed an unusual arrangement of chain fibre nuclei. Other, inconstant proprioceptors included tendon endings, Ruffini endings, Pacinian corpuscles, paciniform and lamellated endings. Topologically, the endings other than spindles were extramuscular, so that the overall pattern of proprioceptive innervation resembled that of skeletal muscle in general.

Lingual nerve section was without apparent effect on the proprioceptors. Section of the hypoglossal nerve at its point of entry into the tongue caused severe depletion of ipsilateral proprioceptors and of fusimotor nerves. In the anterior tongue there was evidence of transmedian overlap by efferent and afferent axons contained in the hypoglossal nerve. Hypoglossal section at the skull base caused degeneration of fusimotor nerves but not of proprioceptors.

Section of (*a*), the connexion of C2–C3 ventral rami with the hypoglossal, together with section of (*b*), the ramus descendens hypoglossi, caused depletion of lingual proprioceptors; again there was evidence of transmedian overlap. Procedures (*a*) or (*b*) alone had a lesser effect. It was concluded that lingual proprioceptive afferent fibres occupy the distal hypoglossal nerve, leaving it in the ramus descendens and in the C2–C3 connexion to enter the spinal cord via nerves C2 and C3.

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