J. Physiol. (1956) 133, 420–432

A FUNCTIONAL ANALYSIS OF THE MYELINATED FIBRES OF THE SUPERIOR LARYNGEAL NERVE OF THE RAT

By B. L. ANDREW

From the Department of Physiology, Queen's College, Dundee, University of St Andrews

(*Received* 9 *April* 1956)

The main features of the distribution of the sensory and motor fibres from the vagus into the laryngeal nerves are well known and have been established by histological methods (DuBois & Foley, 1936, 1937). Some of the sensations subserved by fibres in the superior laryngeal nerve have been determined by electrical stimulation of the nerve in man (Ogura & Lam, 1953). Less is known of those afferents which do not give rise to sensation, and the numerous studies which have demonstrated reflex effects of stimulation of the superior laryngeal nerve (e.g. Sjöblom, 1915; Johnson, 1935; Andersson, Landgren, Neil & Zotterman, 1950; Doty, 1951) do not directly indicate the type of afferent involved.

Table 1. Sensory fibres which have been detected in the superior laryngeal nerve of the rat

Afferent	Location of the endings	Reference
Baroceptor	Aortic arch	Andrew (1954*a*)
Muscle-sense	Oesophagus	Andrew (1954*a*)
Joint proprioceptor	Thyroepiglottic joint	Andrew (1954*b*)
Chemoreceptor	Taste buds on epiglottis	Andrew & Oliver (1951)
Touch receptor	Mucosa rostral to vocal cords	Andrew & Oliver (1951)

Nerve action potential studies on the superior laryngeal nerve have indicated the presence of a variety of functionally different afferents and efferents. The types of afferent already described in the rat are given in Table 1. When electrical recordings are made from multifibre preparations it is sometimes possible to draw inferences concerning the relative calibres of the active fibres from the differences in action potential size. The branches of the main trunk are functionally specialized, e.g. the motor fibres to the cricothyroid muscle are all contained in a single branch, and their histological character, in terms of fibre size distribution, is different. In the present paper an account is given of the functional groups detected and of an attempt to associate such groups with ranges of fibre size.

METHODS

The experiments were performed on forty rats. Anaesthesia was induced with trichloro-ethylene vapour and maintained by intraperitoneal injection of 25% urethane solution (w/v), 5 ml./kg body weight.

The dissection of the superior laryngeal nerve. A mid-line incision was made on the ventral surface of the neck. The subcutaneous tissue was divided between the salivary glands. The sternohyoid muscle was cut transversely at its attachment to the hyoid bone and reflected back and cut short, close to the sternum. The edges of the wound were tied back and the cavity so formed filled with paraffin oil. All further dissection was carried out beneath the oil surface. The omohyoid muscle was detached from the hyoid bone, and in many experiments it was found convenient to detach the sternothyroid muscle from the thyroid cartilage, to reveal the smaller branches of the superior laryngeal nerve. For experiments in which recordings were made from nerve branches within the thyroid cartilage, a tracheal cannula was inserted and the hyoid bone and part of the thyroid cartilage were removed. An aperture was made in the ventral wall of the pharynx, so as to give access to the epiglottis for stimulation purposes.

Recording. As the wound cavity was small, and as in some experiments two pairs of electrodes had to be used very close to each other, some care was necessary in the choice of the electrode dimensions, and the design of the manipulators. The electrodes used consisted of bright silver wires, diameter 0·1 mm, enclosed, except for 3–4 mm at the tip, in hard glass tubes, outside diameter 1 mm. The electrodes were connected to conventional capacity-coupled amplifiers and thence to cathode-ray oscillographs and loudspeaker. The action potentials were recorded on moving bromide paper.

Histology. Osmic acid vapour was used to fix and stain the nerve trunks. The nerves were tied out under slight tension to a rectangular frame made of glass rod, and placed on a platform a few millimetres above the surface of a 2% solution (w/v) of osmic acid in a closed dark-glass jar for 12–18 hr. They were washed for 3–6 hr, dehydrated and embedded in paraffin wax. Sections were cut at thickness 5–7μ. Preparations were photographed directly on to bromide paper at a magnification of 1000. Measurements were made of the external diameter of the myelin sheath by comparing the photographic image with circles of 2, 4, 6, 8, 10 mm drilled in a Perspex sheet. The sources of error which may be introduced in measurements of this kind have been discussed in the reports of Gutmann & Sanders (1943), Aitken, Sharman & Young (1947), Sanders (1948) and Evans & Vizoso (1951).

RESULTS

The macroscopic anatomy of the superior laryngeal nerve

The nerve runs as a single trunk from the caudal pole of the nodose ganglion to a point a few millimetres from the thyroid cartilage, where it divides to form Branch 1 which is the equivalent of the internal laryngeal nerve. This branch penetrates the thyroid cartilage and innervates the larynx above the level of the vocal cords. The remainder of the trunk now divides into Branch 2 which contains the motor fibres to the cricothyroid muscle, and Branch 3 which innervates the larynx below the level of the vocal cords and the oesophagus. Branch 4 emerges from Branch 3 and is sometimes difficult to identify as a separate filament, but it ultimately forms part of the anastomosing branch between the superior and recurrent laryngeal nerves. Some of the features of Branch 4 have already been described (Andrew, 1954*a*); it contains fibres innervating the oesophagus and aortic arch. The branch to the thyroid gland

was not recognized anatomically, but fibres from the gland were detected electrically in the main trunk. The anatomy of the connexion between the thyroid gland and the superior laryngeal nerve in the dog has been described by Nonidez (1931, 1935).

Correlation between nerve impulse size and fibre composition of the main trunk and branches

It is generally accepted that the size of the recorded action potential of a nerve fibre, when conventional wire electrodes on the surface of the trunk are used to pick up the potential, is determined partly by the diameter of the fibre. Thus the relative sizes of the action potentials of two fibres in the same trunk may be used as a guide to relative fibre diameter, but the action potentials of nerve fibres from different preparations may not be usefully compared, since other factors, such as the electrical shunting effect of other tissue, are not necessarily operating similarly. The validity of these assumptions has been examined and supported by Hunt (1951), in a study of the action potentials of large and small muscle efferents. It was stressed in that paper that if differential damage to nerve fibres in the trunk occurred, then the relative action potential sizes were no guide to fibre size; for this reason it is preferable to use naturally occurring nerve branches rather than filaments dissected from a nerve trunk, since the fibres in the latter are so much more vulnerable. Where there is any doubt about the condition of the nerve, use may be made of the fact that in an undamaged nerve an alteration of electrode spacing, or an equal shift of both electrodes in one direction should not markedly change the relative sizes of action potentials from different fibres. In the present experiments conclusions about the relative size of fibres carrying different modalities of sensation, or functionally different types of motor innervation, were drawn only when consistent relative differences in action potential size from a number of preparations were obtained. When external wire electrodes are applied to a nerve trunk containing several hundred fibres, only a small proportion of the active fibres are electrically accessible to the electrodes; indeed if this were not so, the record would be very confused owing to electrical summation of numbers of simultaneous nerve impulses in different active fibres. To examine more than this small number of accessible fibres it is necessary to dissect the nerve into very much smaller filaments. These dissections are useful, in spite of the risk of differential damage, as they permit comparisons of action potential size between functional groups not found together in the smaller branches of the nerve. Thus the record in Fig. 7 was obtained from a preparation containing afferents from Branch 4 (aortic baroceptors) and Branch 1 (stretch receptors). Dissection of the main trunk was also necessary for the examination of the afferents from the thyroid gland, as the branch carrying these fibres was not recognized anatomically.

The fibre composition of the main trunk. The total number of myelinated fibres in the main trunk was measured in five nerves and the counts were 543, 646, 673, 676 and 825. In the cat, DuBois & Foley (1936) found 2188 and 2776 fibres from osmic acid preparations. Ogura & Lam (1953) reported 15,000 myelinated fibres in the human nerve. In the rat the majority of the fibres were less than 4μ in diameter. The fibre distribution of a typical nerve is shown in Fig. 1. Fibres above 10μ in diameter were rare. Groups of ganglion cells were found distributed along the nerve.

Recordings from the central end of the main trunk. The records were dominated by action potentials in motor fibres coursing to the cricothyroid muscle. Motor impulses to the oesophageal muscle were obscured.

Recordings from the peripheral end of the main trunk. The largest action potentials detectable were connected to stretch receptors (including joint proprioceptors) located in the larynx rostral to the vocal cords. Further information was obtained by sequential detachment of the branches from the trunk and the results are summarized in Table 2.

The fibre composition of Branch 1. Fibre counts were made of five specimens of this branch and totals of 218, 262, 279, 294 and 339 were obtained. In three of these specimens, counts for the main trunk were available and showed that Branch 1 accounted numerically for 44, 41 and 41% of the fibres in the main trunk. A histogram of the distribution of the fibres by size in this branch is given in Fig. 2. It will be seen that nearly all the smallest ($<2\mu$) fibres in the main trunk enter Branch 1, together with a variable fraction of the fibres of other sizes.

Recordings from the central end of Branch 1. No large fibre discharges were detected either at rest or during swallowing movements. Small fibre discharges in a few fibres at low frequencies were just detectable.

Recordings from the peripheral end of Branch 1. The record was dominated by continuous and phasic discharges from stretch receptors and joint proprioceptors. An account of the behaviour of these joint proprioceptors has been given elsewhere (Andrew, 1954*b*). The stretch receptors, other than those associated with the thyroepiglottic joint, were difficult to localize owing to the mechanical interdependence of the many parts which make up the mammalian larynx. Some discharged during inspiration, others during expiration, during vigorous breathing some were found with a frequency maximum during both the inspiratory and the expiratory phase of respiration, others discharged at an almost steady frequency throughout the cycle. It seemed likely that the stimulus for some of the fibres which discharged during expiration was the tension produced in structures associated with the glottis when the latter obstructed the outflow of air. Fig. 5 gives an example of discharge in a fibre connected to an ending stimulated during expiration. The activity of the smaller fibres could be detected only after detachment of the

TABLE 2. Relative action potential sizes recorded from the peripheral end of the main trunk

Preparation	Detectable activity in the main trunk
All branches intact	Record dominated by joint proprioceptor and stretch receptor impulses from Branch 1
Branch 1 detached	Largest impulses detectable are from aortic baroceptor fibres from Branch 4
Branches 1 and 4 detached	Sensory impulses from Branch 3 just detectable

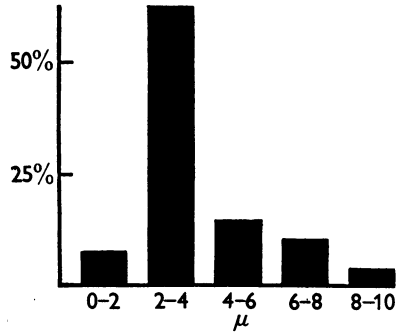

Fig. 1.

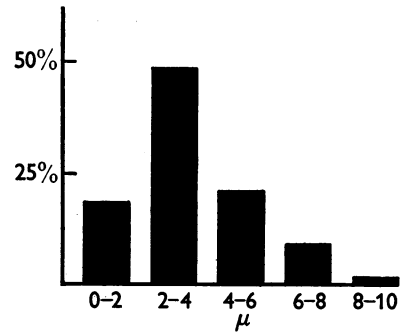

Fig. 2.

Fig. 1. The composition in terms of myelinated fibre size, of the main trunk of the superior laryngeal nerve of the rat. The total number of fibres in this specimen was 825.

Fig. 2. The composition, in terms of myelinated fibre size, of Branch 1 of the superior laryngeal nerve of the rat. The total number of fibres in this specimen was 339.

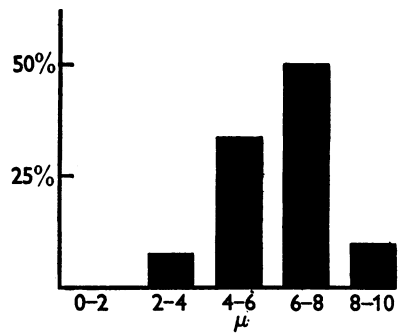

Fig. 3.

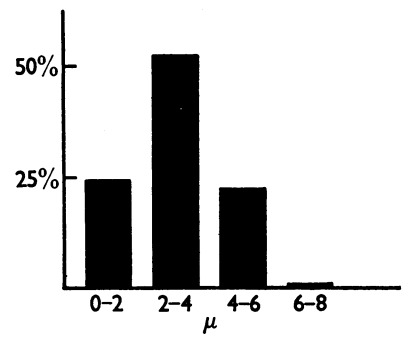

Fig. 4.

Fig. 3. The composition, in terms of myelinated fibre size, of Branch 2 of the superior laryngeal nerve of the rat. The total number of fibres in this specimen was 78.

Fig. 4. The composition, in terms of myelinated fibre size, of Branch 3 of the superior laryngeal nerve of the rat. The total number of fibres in this specimen was 160.

branches of Branch 1 which contained the proprioceptor fibres. This was achieved by removing part of the wing of the thyroid cartilage, and detaching branches of Branch 1 which serve the thyroepiglottic joint and lateral epiglottic folds. Nerve impulses in fibres connected by rapidly adapting touch endings in the mucosa of the epiglottis could now be distinguished, and also slowly adapting discharges from chemoreceptors sensitive to sodium chloride solutions.

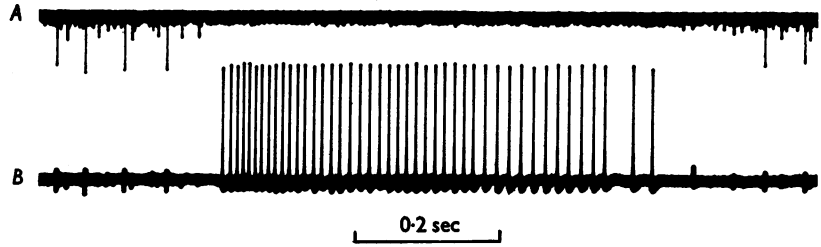

Fig. 5. Simultaneous recordings *A*, of the electromyogram of motor units in the cricothyroid muscle, and *B*, from a filament dissected from the peripheral end of the superior laryngeal nerve of the rat. The recording *A* is included as it indicates the timing of the respiratory cycle; the muscle is active during inspiration. The nerve fibre in record *B* is thus seen to be connected to an ending stimulated during expiration.

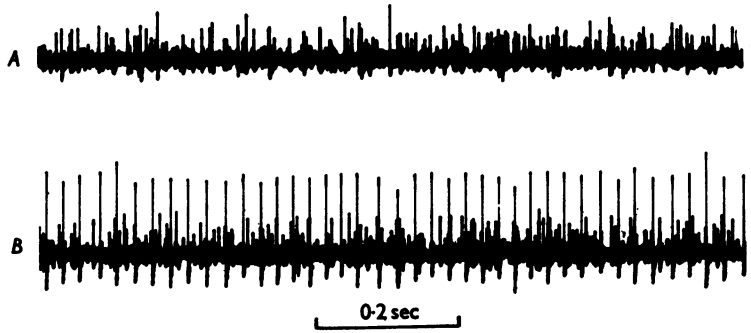

Fig. 6. Branch 1 has been picked up within the thyroid cartilage and its branches to the thyroepiglottic joint have been cut. Endings in the mucosa of the epiglottis have been stimulated with a crystal of sodium chloride a minute before the records were taken. The slowly adapting irregular discharge in small fibres produced by this stimulus is shown in record *A*. In record *B*, in addition to the discharge in small fibres, a larger fibre connected to a slowly adapting stretch receptor has been brought into activity by mechanical stimulation of the epiglottis.

It should be noted that endings sensitive to sodium chloride solutions are not necessarily taste buds, and endings mediating the common chemical sensitivity of the mucous membrane probably participate as well. The detected amplitude of impulses in the chemoreceptor fibres was less than half that of the largest stretch-receptor fibres, and showed the characteristic irregularity of discharge associated with taste endings (see Fig. 6).

The fibre composition of Branch 2. Five specimens were examined and totals of 58, 65, 70, 78 and 82 fibres were obtained. There were a few small fibres in the $<4\mu$ group, the majority, however, lay in the 4–8μ or 6–10μ groups. A histogram of the fibre-size distribution in a typical nerve is shown in Fig. 3.

Recordings from the central end of Branch 2. The record was dominated by impulses of large amplitude in fibres innervating the cricothyroid muscle. This muscle has an accessory respiratory function and exerts maximum tension during inspiration. Some of the motor neurones discharge only during inspiration and others continuously, with a maximum frequency during inspiration. During increased respiratory activity the number of units discharging continuously rises. The large fibre discharge in the nerve was similar to the detectable activity in the fully innervated muscle. It was not possible to decide whether small fibre efferents were present, as no method of selectively interrupting the outflow in the large fibres was available.

Recordings from the peripheral end of Branch 2. No large fibre muscle proprioceptor or stretch receptor discharges were detected. Some evidence was obtained that small fibre afferents from the mucosa of the laryngeal cavity below the level of the vocal cords were present in this nerve.

The fibre composition of Branch 3. Three specimens of this branch were examined and totals of 160, 183 and 334 fibres were obtained. It was found to be composed entirely of small fibres; 75–100% were in $<4\mu$ group with the remainder in the 4–6μ group. A histogram of the fibre size distribution of one of the nerves is shown in Fig. 4. This nerve had a single fibre larger than 6μ.

Recordings from the central end of Branch 3. Continuous activity in efferents at low frequencies (10–20 imp./sec) was usually detectable. The amplitude of the action potentials was small and the frequency was usually slightly modulated by the respiratory rhythm, the maximum occurring during inspiration. In some preparations a few impulses were discharged phasically during inspiration, the level of activity in these fibres following that of the inspiratory centre. During the pharyngeal phase of a swallowing movement, activity in these fibres was inhibited, and then resumed (together with that of the other accessory respiratory muscles) at a slightly increased level, which declined to the resting level during the succeeding few seconds. Other fibres were found to be present which became active only during swallowing when a propulsive wave moved down the cervical part of the oesophagus. The amplitude of these action potentials was as small as, or smaller than, those in the previously described continuously discharging fibres.

Recordings from the peripheral end of Branch 3. Continuous activity in a few fibres of small action potential was detectable. The passage of a propulsive wave down the cervical oesophagus was associated with a multifibre volley of afferent impulses of small amplitude. Direct stimulation of the oesophagus

with a probe gave rise to afferent small-fibre discharges. Fig. 8 gives an indication of the size of the impulses relative to aortic baroceptor impulses.

The fibre composition of Branch 4. This was variable in size and only one good histological preparation was obtained; this contained forty fibres of which thirty were in the $<4\mu$ group and the rest in the $4–6\mu$ group.

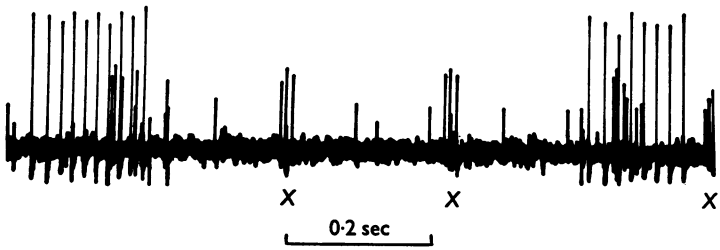

Fig. 7. A recording from a filament dissected from the peripheral end of the main trunk of the superior laryngeal nerve. The grouped impulses marked X are from an aortic baroceptor fibre. The larger impulses are from a fibre connected to a stretch receptor which discharged a train of impulses during each inspiration.

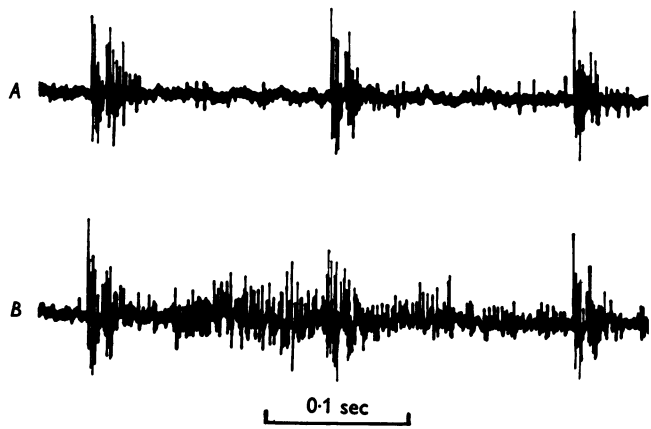

Fig. 8. Two recordings from the peripheral end of a nerve composed of Branches 3 and 4. Record *A*, normal, showing multifibre volleys in baroceptor fibres at each heart beat. *B*, a record taken as a propulsive wave moved down the cervical oesophagus. Note the additional multifibre volley lasting about a third of a second.

Recordings from the central end of Branch 4. To obtain a suitable length of nerve it was necessary to dissect the thyroid gland away from the trachea so as to reveal the filament connecting the superior to the recurrent laryngeal nerve. This was detached from the recurrent laryngeal nerve and dissected free from the thyroid gland. A small number of continuously discharging efferents was detected. The discharges were regular at frequencies in the range 8–15 imp./sec, but they did not cease during the pharyngeal phase of a swallowing movement, and so could be distinguished from the continuously discharging

efferents of Branch 3. In addition, small fibre efferents were detected which became active during the passage of a propulsive wave down the cervical oesophagus.

Recordings from the peripheral end of Branch 4. Features of the impulse traffic in this branch have been described elsewhere (Andrew, 1954*a*). Fig. 8 relates the recorded action potential size of the aortic baroceptor fibres to the oesophageal afferents, and Fig. 7 relates the size of the large-fibre stretch-receptor afferents in Branch 1 to the aortic baroceptor afferents. The latter record was obtained from a filament dissected from the peripheral end of the main trunk.

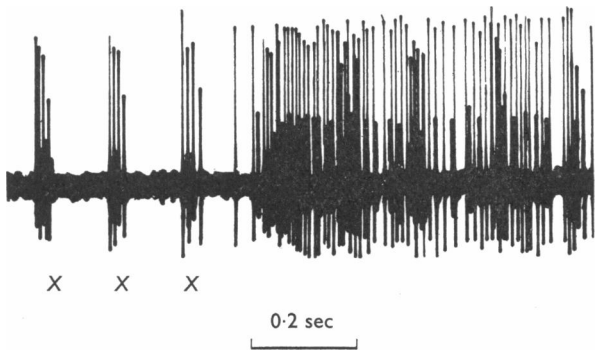

Fig. 9. A recording from a filament dissected from the peripheral end of the main trunk of the superior laryngeal nerve. The grouped impulses marked X are from an aortic baroceptor fibre. The continuous discharge which occupies the right-hand part of the record arose in other fibres contained in the preparation in response to probing a highly localized area of the thyroid gland.

Afferent fibres from the thyroid gland. These fibres were detected in the main trunk and were found to be connected to slowly and rapidly adapting mechano-receptors in the thyroid gland. Exploration of the gland with a fine probe revealed highly localized zones in the lobes and isthmus where action potentials could be generated. A resting discharge was not detected in these fibres. The action potential size was about the same as that of the aortic baroceptor fibres. Fig. 9 shows a record from a preparation from the peripheral end of the main trunk which contained afferents from the thyroid mechanoreceptors and aortic baroceptors.

DISCUSSION

In this work an attempt has been made to answer two questions: first, which functions, motor and sensory, are served by the myelinated fibres in the superior laryngeal nerve and secondly, is it possible to associate functional groups of fibres with ranges of fibre size? It was realized that if there were any complete functional groups of fibres, either motor or sensory, which remained

inactive, or electrically undetectable, throughout the experiments, serious errors might be introduced, since the histological description of the nerve, which is complete, is necessarily equated against the electrophysiological information which could only be assumed to be complete. Records taken during swallowing movements were, of course, essential since some fibres only become active during these movements, but there may be fibres which were not made active by any of the stimuli applied. The features of the activity of those groups which participate in swallowing will be described in more detail elsewhere.

Motor fibres. Branch 2 contains a group of large fibres, but no evidence was obtained that any of these were sensory, and certainly no large amplitude discharges were recorded from the peripheral end of the branch in any experiment. The efferent impulses, moreover, were of large amplitude and the activity of the cricothyroid muscle could be shown to follow the pattern of these impulses. It was concluded that the motor fibres to the cricothyroid muscle are in the 6–10μ group. The motor fibres to the oesophageal muscle must be in a smaller size group since fibres larger than 6μ are rare in Branch 3 and, in confirmation, recordings containing efferents both to the cricothyroid muscle and the oesophageal musculature showed the latter to be associated with action potentials of markedly smaller size. As the sensory fibres present in Branch 3 gave rise to action potentials of about the same size as the motor fibres, and as the fibre size spectrum of the branch is so limited, it seems reasonable to associate the oesophageal motor fibres with the 4–6μ group.

The track taken by the motor fibres to the cricothyroid muscle and the cervical oesophagus varies amongst the common laboratory mammals. The fibres may leave the vagus above or below the nodose ganglion either in company with the pharyngeal or superior laryngeal nerve, or as separate filaments. The reported variations in supply to the cricothyroid muscle have been reviewed previously (Andrew, 1955). In the case of the cervical oesophagus, Hwang, Grossman & Ivy (1948) have made a valuable review of previous work and have determined the anatomical arrangements by stimulation and X-ray methods in the cat, dog, rabbit, monkey, rat and guinea-pig. Their experiments indicated that in the dog and cat the fibres usually leave the vagus with the pharyngeal branch and reach the oesophagus by the pharyngo-oesophageal nerve. This nerve has been previously named, in the dog, the inferior pharyngeal ramus (Nonidez, 1931), and the descending pharyngeal (Lemere, 1932). In the monkey (*Macacus rhesus*), rat and guinea-pig the fibres leave the vagus in the superior laryngeal nerve.

Secretomotor fibres to the mucous glands of the epiglottis and trachea are probably present in all the branches, but conditions are most favourable for their detection in Branch 1, since efferents to skeletal muscle are absent, and histologically small fibres from Branch 1 were seen to enter the mucus-secreting

glands embedded in the epiglottal cartilage. However, although small amplitude efferent impulses were detected in Branch 1 there was no evidence to associate them definitely with secretomotor action.

Sensory fibres. The largest sensory fibres, judged from their action potential size, are found in Branch 1 and are connected to stretch receptors and joint proprioceptors. Since no large fibre efferents were detected in Branch 1 it was assumed that these sensory fibres had the largest fibre diameters found histologically in the branch, i.e. within the group 6–10μ. The fibres from fast touch endings in the mucosa of the epiglottis were of similar or rather smaller action potential and were assumed also to be in the 6–10μ group. The chemoreceptor

TABLE 3. Functional components of the superior laryngeal nerve and its branches

Branch	Afferent fibres	Efferent fibres
1	Joint proprioceptors Stretch receptors Fast touch Chemoreceptors (epiglottal) Common chemical sense	Small fibres, probably including secretomotor
2	Small fibre mucosal endings	Large fibres to cricothyroid muscle
3	Oesophageal muscle sense	Small fibres, motor to oesophageal muscle
4	Aortic baroceptors Oesophageal muscle sense	Motor to oesophageal muscle Small fibre efferents, function unknown
Thyroid branch	Mechanoreceptors in thyroid gland	—

TABLE 4. Functional groups arranged in descending order of fibre size

10–6μ	Cricothyroid muscle efferents Stretch receptors (Branch 1) Joint proprioceptors (Branch 1) Fast touch (Branch 1)
About 6μ	Aortic baroceptors Thyroid mechanoreceptors
Less than 6μ	Epiglottal chemoreceptors Oesophageal muscle efferents and afferents Secretomotor (?) in Branch 1 Efferents (Branch 4) function unknown Mucosal endings (Branch 2)

or common chemical sense fibres were of markedly smaller size and consigned to the $<6\mu$ group. The action potentials of the sensory fibres from the oesophagus, as mentioned earlier, were found to be in the same category as those of the oesophageal efferents and hence the fibres are in the $<6\mu$ group. The aortic baroceptor afferents in Branch 4 gave smaller action potentials than the large branch 1 afferents, but equal or larger potentials than the oesophageal afferents in Branches 3 and 4, and so were assumed to occupy a middle position in the size spectrum, i.e. about 6μ. The larger slowly adapting mechanoreceptors of the thyroid gland appeared to be in the same category. Detection of these fibres in the main trunk confirms a prediction made on histological grounds by Nonidez (1931, 1935) that part of the contribution of the superior laryngeal

nerve to the thyroid nerve is sensory. The function of such mechanoreceptors within the gland is not clear, they are rather deep for an exteroceptive use; the possibility that the slowly adapting endings might signal a raised intraglandular pressure is interesting but not easy to test in acute experiments.

An attempt has been made in Tables 3 and 4 to summarize the answers to the two questions given at the beginning of this discussion. Further information is clearly required on the small afferent fibres serving the mucosa below the vocal cords, and an analysis of the types of ending in the wall of the cervical oesophagus would be valuable. The presence of sensory endings capable of sustaining or initiating a propulsive wave in the oesophagus has been known for many years from the results of experiments on the mechanism of swallowing. Meltzer (1899) has reviewed the early literature, but the small size of the afferent fibres makes the electrical examination rather difficult.

SUMMARY

1. The superior laryngeal nerve of the rat and its branches were examined histologically with osmic acid and their composition in terms of fibre size was determined.

2. Impulse traffic in efferent and afferent fibres was recorded from the anaesthetized animal and the relative action potential sizes of fibres serving different motor and sensory functions described.

3. The action potential size of the functional groups was correlated with the fibre composition of the nerve branches. Control of the fibres of the cricothyroid and oesophageal muscle was carried out by nerve fibres in the ranges 6–10μ and $<6\mu$ respectively.

4. A wide variety of sensory fibres was detected, including joint proprioceptor, stretch receptor, fast touch, chemoreceptor, aortic baroceptor, thyroid gland mechanoreceptor, and oesophageal muscle sense. Suggestions were made as to the relative fibre sizes of these groups.

I wish to thank Professor G. H. Bell for his interest in this work. I also wish to thank Mrs L. Leithead for her skilled assistance in the production of the osmic acid preparations.

REFERENCES

AITKEN, J. T., SHARMAN, M. & YOUNG, J. Z. (1947). Maturation of regenerating nerve fibres with various peripheral connexions. *J. Anat., Lond.*, **81**, 1–22.

ANDERSSON, B., LANDGREN, S., NEIL, E. & ZOTTERMAN, Y. (1950). Reflex augmentation of intestinal motility caused by stimulation of the superior laryngeal nerve. *Acta physiol. scand.* **20**, 253–257.

ANDREW, B. L. (1954*a*). A laryngeal pathway for aortic baroceptor impulses. *J. Physiol.* **125**, 352–360.

ANDREW, B. L. (1954*b*). Proprioception at the joint of the epiglottis of the rat. *J. Physiol.* **126**, 407–523.

ANDREW, B. L. (1955). The respiratory displacement of the larynx: a study of the innervation of accessory respiratory muscles. *J. Physiol.* **130**, 474–487.

ANDREW, B. L. & OLIVER, J. (1951). The epiglottal taste buds of the rat. *J. Physiol.* **114**, 48*P*.

DOTY, R. W. (1951). Influence of stimulus pattern on reflex deglutition. *Amer. J. Physiol.* **166**, 142–158.

DUBOIS, F. S. & FOLEY, J. O. (1936). Experimental studies on the vagus and spinal accessory nerves in the cat. *Anat. Rec.* **64**, 285–307.

DUBOIS, F. S. & FOLEY, J. C. (1937). Quantitative studies of the vagus nerve in the cat. II. The ratio of jugular to nodose fibres. *J. comp. Neurol.* **67**, 69–87.

EVANS, D. H. L. & VIZOSO, A. D. (1951). Observations on the mode of growth of motor nerve fibres in rabbits during post-natal development. *J. comp. Neurol.* **95**, 429–462.

GUTMANN, E. & SANDERS, F. K. (1943). Recovery of fibre numbers and diameters in the regeneration of peripheral nerves. *J. Physiol.* **101**, 489–518.

HUNT, C. C. (1951). The reflex activity of mammalian small-nerve fibres. *J. Physiol.* **115**, 456–469.

HWANG, K., GROSSMAN, M. I. & IVY, A. C. (1948). Nervous control of the cervical portion of the oesophagus. *Amer. J. Physiol.* **154**, 343–357.

JOHNSON, J. (1935). Effect of superior laryngeal nerves on tracheal mucus. *Ann. Surg.* **101**, 494–499.

LEMERE, F. (1932). Innervation of the larynx I. Innervation of the laryngeal muscles. *Amer. J. Anat.* **51**, 417–438.

MELTZER, S. J. (1899). On the causes of the orderly progress of the peristaltic movements in the oesophagus. *Amer. J. Physiol.* **2**, 266–272.

NONIDEZ, J. F. (1931). Innervation of the thyroid gland. II. Origin and course of the thyroid nerves in the dog. *Amer. J. Anat.* **48**, 299–329.

NONIDEZ, J. F. (1935). Innervation of the thyroid gland. III. Distribution and termination of the nerve fibres in the dog. *Amer. J. Anat.* **57**, 135–169.

OGURA, J. H. & LAM, R. L. (1953). Anatomical and physiological correlations on stimulating the human superior laryngeal nerve. *Laryngoscope*, **63**, 947–959.

SANDERS, F. K. (1948). The thickness of the myelin sheaths of normal and regenerating peripheral nerve fibres. *Proc. Roy. Soc.* B, **135**, 323–357.

SJÖBLOM, J. C. (1915). Experimentelle Untersuchungen über den Einfluss einiger zentripetaler Nerven auf die Atmung. *Skand. Arch. Physiol.* **32**, 1–114.