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## PROPRIOCEPTION AT THE JOINT OF THE EPIGLOTTIS OF THE RAT

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Usually the problem of joint proprioception is divided into two parts. The first part is concerned with the behaviour of joint proprioceptive endings when the joint is motionless or during passive movements produced by externally applied forces. The impulse discharges from the knee-joint of the cat have been studied in this way by Andrew & Dodt (1953), Boyd & Roberts (1953) and Andrew (1954*a*). The second part of the problem is concerned with the sensory inflow from joint proprioceptors when movements are produced by the musculature of the animal. This is less readily studied, as it is difficult to produce normal limb movements in the anaesthetized animal.

The laryngeal joints seemed well suited for experiments on the second part of the problem since movements occur regularly with respiration in the anaesthetized animal. In addition, the amplitude of the movements is variable to a certain extent as dyspnoea is accompanied by an increase in the vigour of the accessory respiratory movements. Some preliminary experiments have already been described (Andrew & Oliver, 1951). On the other hand, the joint is not easily studied from the point of view of static performance since it cannot be immobilized conveniently; even if the motor fibres to the laryngeal muscles are cut the respiratory movements of the tongue, pharynx and trachea disturb the joint. For this reason records of the discharge from the static or passively moved joint were made from an isolated larynx preparation. Compared with other joints the task of localizing the nerve endings is simplified since there are no bony structures to contend with during dissection, and it is not necessary to decalcify the histological preparations.

### METHODS

The experiments were performed on thirty rats. The animals were anaesthetized with urethane, given intraperitoneally as a 25% (w/v) solution, 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 connective tissue in the region of the common carotid artery at the level of the thyroid cartilage was dissected with the aid of a low-power binocular microscope to reveal the superior laryngeal nerve at its point of departure from the nodose ganglion. The nerve was detached from the ganglion and dissected free in the direction of the larynx. The nerve divides usually into four filaments as it approaches the larynx.

*Recording.* The prepared nerve was placed on silver wire electrodes which were bound with a single layer of silk wound spirally to maintain a layer of Locke's solution on the surface of the wire. A pool of Locke's solution was formed at the bottom of the wound cavity and the nerve and the electrodes were submerged in this except when recordings were taking place. The electrodes were connected to a conventional capacity-coupled amplifier and thence to cathode-ray oscillographs and loudspeaker. The action potentials were recorded on moving bromide paper. In those experiments in which the respiratory movements were recorded simultaneously with action potentials either a stethograph was passed round the body of the rat at the level of the diaphragm and the tensions which were developed were applied to a piezoelectric crystal, or a small plate was laid over the region of the xiphisternum and its movements transmitted by a lever to the piezoelectric crystal. The voltages developed by the crystal were fed into a cathode-follower stage. The cathode-follower output after a single stage of d.c. amplification was applied directly to a deflector plate of one of the two beams of the recording cathode-ray oscillograph. When the electromyogram of the epiglottic muscle was recorded, the mid-line overlying part of the hyoid bone was excised and silver wire electrodes applied to the muscle. The potentials were amplified and applied to the second beam of the recording cathode-ray oscillograph.

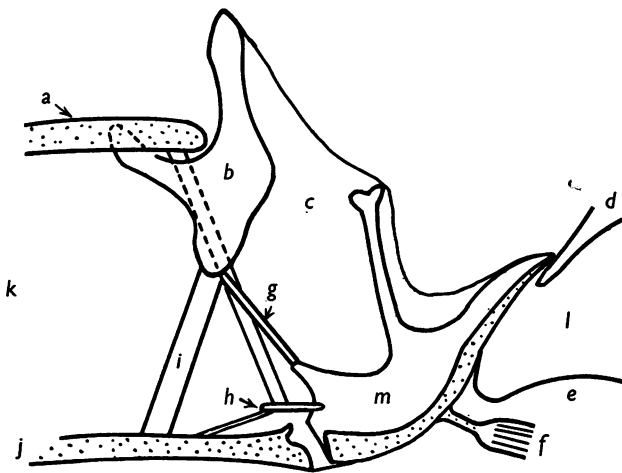
*The isolated larynx preparation.* The larynx, together with a short piece of trachea, was dissected out of the anaesthetized animal or immediately after the animal had been killed by a blow and placed in a bath of warm oxygenated Locke's solution. The larynx was secured by tying a glass tube into the tracheal stump and oxygen was passed through the tube, escaping into the bath through the glottis. Additional oxygenation was provided by a sintered-glass gas distributor in the bath. As the gas bubbles stimulated nerve endings in the preparation the gas supply was cut off during tests. Anoxia of the larynx showed itself by a gradual failure of endings, though some endings were found to be much more vulnerable than others. The bath was kept warm by a direct current in a glass-enclosed resistance element immersed in the Locke's solution.

*Histology.* The morphology of the endings and the arrangement of the sensory axons were studied with methylene blue. The tissues were stained by perfusion of the blood vessels with a solution containing, per 100 ml., 0.8 g NaCl, 0.15 g MgBr<sub>2</sub>, 0.02 g methylene blue, 0.2 g glucose dissolved in distilled water. It was found convenient to cannulate one common carotid artery and inject 5 ml. into the peripheral end. The branches of the common carotid artery, apart from those serving the larynx, were tied off prior to the injection. The injection was then repeated on the other side. After an interval of about 10 min the larynx was excised and placed in a shallow dish containing a solution of similar composition to the staining fluid except that the methylene blue was omitted. It was trimmed under a dissecting microscope, and when the correct contrast between nerves and other tissues had developed it was immersed in cold saturated ammonium molybdate solution for 12–24 hr. When small pieces of tissue were excised for histological examination in experiments designed to associate stretch sensitivity with specific structures, the small fragments were stained by immersion in the staining fluid for 15 min. It was usually found essential to tie-out these fragments with fine thread to a glass cover-slip so as to preserve their shape and permit recognition of the position of the endings. After fixation the tissues were washed in distilled water for 1 hr, cooled to about 5° C and dehydrated in cold absolute alcohol in the refrigerator at 0–3° C for 3–12 hr. The tissues were then transferred to ice-cold xylol and allowed to warm to room temperature. When they had cleared they were mounted in D.P.X. It usually took several days for the mounting medium to penetrate evenly through the tissues. Microphotographs were taken in orange-coloured transmitted light using Ilford filter micro 5.

## RESULTS

*The mechanism of the thyroepiglottic joint*

The main features of the joint are indicated in Text-fig. 1. The epiglottis has a simple hinge with the thyroid cartilage. The flexion movement of the joint is checked when the epiglottis strikes the arytenoids and the extension movement is normally checked when the ventral surface of the epiglottis strikes the nasal surface of the soft palate: though it is possible for the epiglottis to slip past the soft palate so as to lie in a more extended position with its tip in the space between the buccal surface of the soft palate and the dorsal surface of the tongue. Apart from these extreme checks there are a number of



Text-fig. 1. A diagram of a mid-line longitudinal section through the joint between the epiglottis and the thyroid cartilages in the rat. (a) cricoid cartilage, (b) arytenoid cartilage, (c) lateral aryepiglottic fold, (d) soft palate, (e) tongue, (f) epiglottic muscle, (g) aryepiglottic ligament, (h) cuneiform cartilage, (i) vocal folds, (j) thyroid cartilage, (k) trachea, (l) mouth, (m) epiglottis.

structures which provide a graded opposition as the joint is moved from the position of rest, which is nearer extension than flexion in the isolated joint, either towards flexion or extension. During flexion the epiglottic muscle and the aryepiglottic ligament are stretched. The aryepiglottic ligament is attached to a spur of the epiglottic cartilage. The point of the spur describes an arc during a joint movement and is closest to the tip of the arytenoid at a position intermediate between flexion and extension. During extension the structures, collectively referred to as the cuneiform cartilage system, the aryepiglottic ligament and the lateral aryepiglottic folds, are stretched. The cuneiform cartilage system is shown in Text-fig. 4 and is described in detail later. As is well known, extension or flexion of the joint is produced during

descent or elevation of the larynx as a whole, as occurs during swallowing, but in addition small regular movements occur synchronously with respiration. Movements of the epiglottic muscle, the soft palate, the pharyngeal wall and the thyroid cartilage all influence the position of the joint.

*The isolated larynx preparation*

The use of this preparation allowed the joint to be dissected with much greater ease than *in situ* since control of haemorrhage was no longer a problem and certain parts, such as the dorsal aspect of the larynx, became easily accessible. The preparation was found to be quite reliable, and provided the oxygenation was adequate it functioned for 8–12 hr. In most experiments it was maintained at 30–35° C, but it was found to work at 25° C though the discharge frequencies of the endings were then reduced. Owing to the mechanical stimulation caused by the bubbles of oxygen passing out through the glottis, it was necessary to cut off the gas supply during recordings, but for periods of a few minutes the discharges from the endings were unaffected by the developing oxygen lack. It was considered that details of the performance and location of the sense endings gained from experiments with the isolated joint were necessary in order to interpret the outflow of nerve impulses from the joint *in situ*.

The branches of the superior laryngeal nerve were cut except branch 1, which serves the anterior part of the larynx (Andrew, 1954*b*). When either the main trunk or branch 1 was put on the electrodes a large number of impulses were detectable and clearly many fibres contributed to the sensory outflow. More information was obtained by two procedures; first, limitation of the number of fibres on the electrodes by dissection of the nerve into small strands; and secondly, limitation of the sensory field by section of intralaryngeal branches of the nerve or dissection of the joint tissues. Limitation of the outflow by anoxia occurred in some of the earlier experiments but it was not used deliberately. It was noted that most of the active fibres discharged impulses at steady frequencies when the joint was at rest; no fibres showing a cyclical variation of frequency were detected. Text-fig. 9 shows a comparison between the total discharge in branch 1 of an isolated preparation with that of a larynx *in situ*.

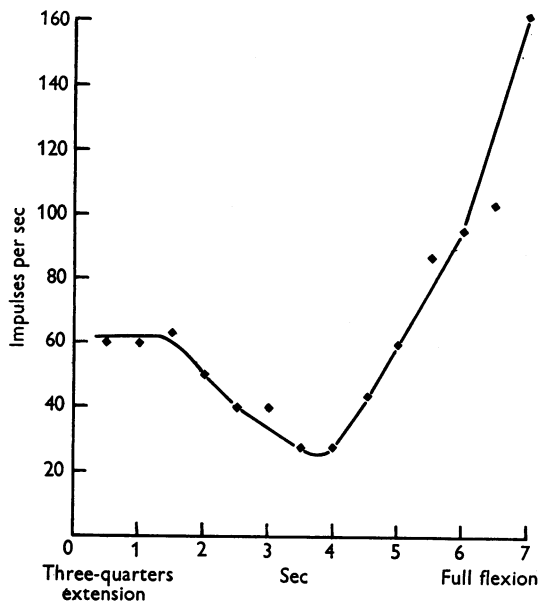
*Endings sensitive to joint position.* These were found to be of two types. The first (type 1) discharged impulses when the joint was between some intermediate position and full extension and the frequency of the discharge rose as extension was approached. The second (type 2) discharged impulses at a frequency which increased as the joint deviated in either direction (flexion or extension) from some intermediate position; as a rule there was no discharge within an arc of joint position on either side of the intermediate position. Text-fig. 2 shows the behaviour of one of these endings but the quiescent

period is concealed in this graph as the points are obtained by counting the impulses in 0.5 sec periods. The pause in the impulse discharge is shown in the recording of another ending of this type in Text-fig. 3.

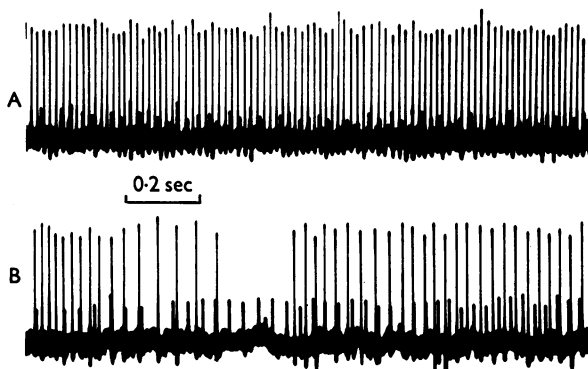
The impulse discharging properties of the endings of the two types proved to be so alike that it was assumed that the same functional ending was responsible for the discharge of both types, but that the difference in sensitivity to joint position was due to anatomical differences of the structures on which the endings were mounted.

*The location of the endings.* Records of fibres attached to type 1 endings were the more easily obtained. The endings were located on the cuneiform cartilage system on the dorsal side of the joint. This system consists of three parts. A band of connective tissue attached to the dorsal surface of the epiglottis over a zone approximately opposite to the attachment on the ventral surface of the tendon of the epiglottic muscle has its other end attached to a U-shaped cartilage (made up of two cuneiform cartilages fused at one end) which lies symmetrically with one limb on each side of the mid-line just anterior to the vocal folds. To each of the limbs of the U-shaped cartilage is attached a slender muscle connected to the cricoid cartilage close to the crico-arytenoid articulation. In addition, a few fibres link the thyroid cartilage to the cuneiform cartilage. The arrangement is shown diagrammatically in Text-fig. 4. The nerve endings are found in two situations. There is a single (sometimes double) ending in the junctional zone where the fibres of the connective tissue band are attached to the cuneiform cartilage. This ending is illustrated in Pl. 1, fig. 2. The other endings lie on the surface of the connective tissue band. The endings in these two sites show histological differences but functional differences were not detected. The positions of the endings on the cuneiform cartilage system were established by removing a piece of cricoid cartilage so that the dorsal surface of the joint could be observed through the dissecting microscope. The joint was then extended to bring into action one or two type 1 endings. Branch 1 was dissected so that a reasonably simple discharge pattern was obtained or alternatively the inessential intralaryngeal branches of branch 1 were cut. The joint was then explored with a fine glass probe for positions where the discharge of the extension receptors was modulated with a minimum of distortion of the tissues. The probe was a very potent stimulus in certain sharply localized positions. When the cuneiform cartilages were excised the extension signalling system was either destroyed or entirely altered in character.

It was considered likely that some, at least, of the type 2 endings were located on the aryepiglottic ligament since it was observed that the ligament had a minimum length in an intermediate position, and was stretched as the joint was extended or flexed, and nerve endings of large fibres were situated on the ligament. In experiments in which all tissue connecting the epiglottis



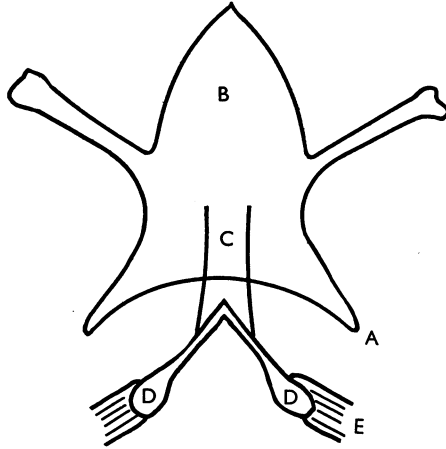
Text-fig. 2. Nerve impulse discharge characteristic of a single type 2 ending in the isolated larynx preparation. The joint was moved from a three-quarter extended position to a fully flexed position. The movement lasted  $5\frac{1}{2}$  sec and began at  $1\frac{1}{2}$  sec on the time scale. The steady impulse discharge frequency of this ending at full extension was 85 imp./sec. Temperature of the bath was  $31^{\circ}$  C. The points on the graph were obtained by counting the number of impulses in  $\frac{1}{2}$  sec periods.



Text-fig. 3. Nerve action potentials from a filament of branch 1 of an isolated larynx preparation. A, the joint is motionless at a three-quarter extended position. The ending is fully adapted and discharging at a steady rate of 62 imp./sec. B, Reading from left to right, the joint is moved towards flexion. The discharge falls in frequency but stops abruptly at about 20 imp./sec; when the discharge starts again it does so at a frequency of about 35 imp./sec. At full flexion (not shown in this figure) the frequency rose to 60 imp./sec.

to the rest of the larynx was cut except the aryepiglottic ligament,<sup>1</sup> tension applied to this remaining tissue initiated a slowly adapting discharge.

*The impulse discharging properties of the endings.* The endings (types 1 and 2) were slowly adapting and maintained their output indefinitely if the fully adapted discharge frequency was above about 10 impulses/sec. If the frequency fell to this level the ending adapted to zero. High frequencies of discharge were maintained for short periods, e.g. 35 impulses in 0.2 sec. The discharge frequency at a given level of stimulation was dependent on temperature.

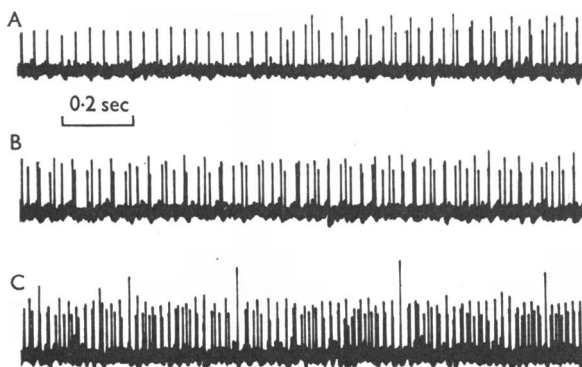


Text-fig. 4. Diagram of plan view of the dorsal surface of the epiglottis and cuneiform cartilages.

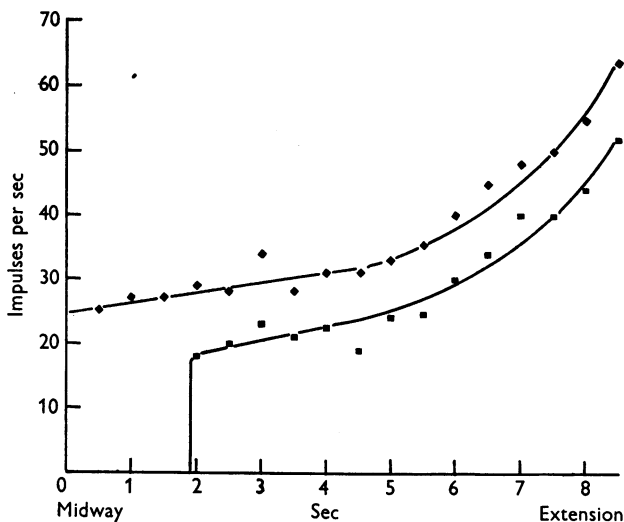
A, a spur of the epiglottis to which the aryepiglottic ligament is attached. B, epiglottis with lateral wings. C, band of connective tissue which secures the cuneiform cartilages to the dorsal surface of the epiglottis. D, cuneiform cartilages fused in the mid-line. E, muscle fibres attached to the cuneiform cartilages. Stretch receptors are found on C, at the junction of C and D, and on the aryepiglottic ligament.

Within the range used in these experiments (25–35° C) the frequency increased with temperature. The anatomical arrangement suggested that stretch is the effective stimulus for the endings; it seems likely that differences in sensitivity are due to different mechanical features of the sites of the endings.

*The performance of endings during joint movements.* Owing to the small size of the joint it was not found possible to devise a stimulator which would move the joint at accurate angular rates. All slow movements of the joint were therefore produced manually with a glass rod applied to the epiglottis. As a consequence the graphs which show the performance of the endings during joint movements are plotted in terms of impulse frequency and time; the time increment being only approximately proportional to angle increment. However, where the nerve filaments contained fibres from more than one active ending, as in Text-fig. 5, it was possible to plot their simultaneous frequencies and this gave an indication of the relative arcs of sensitivity of the endings. Text-fig. 6 gives an example of this. It will be seen that during the slow



Text-fig. 5. Recordings from a small filament of branch 1 of an isolated larynx preparation during a slow extension movement from a mid-way position to full extension. The movement lasted 8 sec and was produced manually. A, at the beginning of the movement, shows the recruitment of a second sensory type 1 ending which begins to discharge at a frequency of 12 imp./sec. B and C, during the periods beginning 4 and 6.5 sec respectively, show the increased frequencies as the joint extends. The large deflexions in record C are not due to the recruitment of a third unit, but are produced by the electrical summation of 2 impulses occurring simultaneously.



Text-fig. 6. The impulse discharging characteristics of the two units shown in Text-fig. 5. Some of the irregularity of the points is presumably due to the fact that the joint was moved manually.



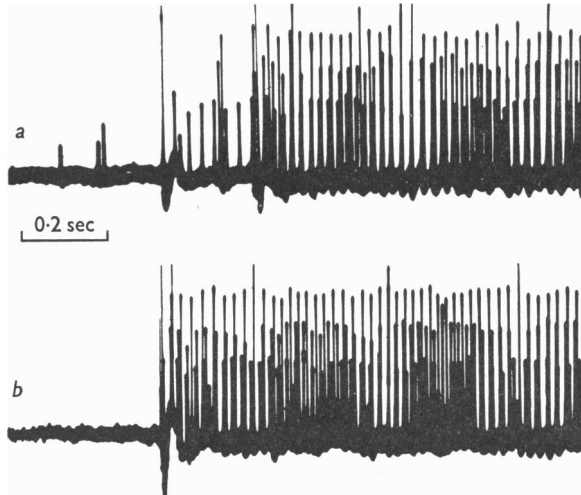
movement the two type 1 endings had different thresholds. The response curves are similar but displaced in time and therefore angle. No multifibre type 2 preparations were obtained, so there is no evidence to offer on this point.

If the joint is moved to extreme flexion and then released, it rapidly moves back to an intermediate position under the action of restoring forces from stretched elastic parts of the joint such as the aryepiglottic ligament. This movement is complete in less than  $\frac{1}{2}$  sec and represents an angular movement of about  $70^\circ$ . It was used to observe the behaviour of the endings during rapid movements, such as occur during swallowing. During these movements the process of recruitment became less obvious, and it appeared that some endings were being stimulated at a point in advance of that at which discharge began during slower movements. Owing to the imprecision of the stimulus this can only be regarded as an impression. Text-fig. 7 shows recordings from a filament containing fibres from three type 1 endings and the spike heights are sufficiently different to avoid confusion. The joint was flexed and allowed to recoil a number of times, and in some records recruitment of the endings was seen as in Text-fig. 7*a*, whereas on other occasions the discharge started almost simultaneously in the three fibres. To give an indication of the adaptation which takes place after such a movement, the graph in Text-fig. 8 has been prepared from a recording of one of the three fibres seen in Text-fig. 7.

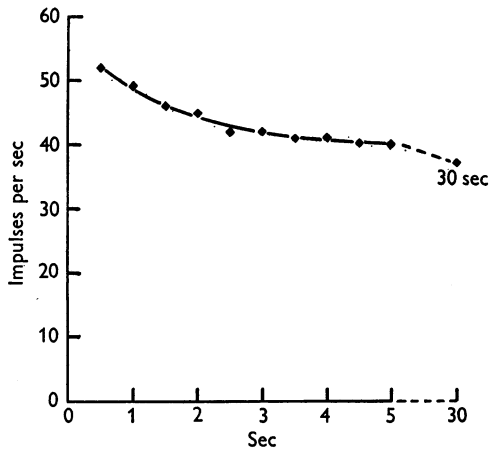
*The sensory outflow from proprioceptors in the anaesthetized preparation*

*Action potentials in the superior laryngeal nerve.* The main trunk contains a variety of sensory fibres, and the activity of the joint proprioceptors is largely obscured by the large volume of sensory impulses. The activity is reduced and simplified when branches 2—4 are cut. Some details of the afferent fibres in these branches have been given elsewhere (Andrew, 1954*b*). After section of these branches the activity contains two conspicuous components. One component consists of large fibres discharging at steady rates, the other of fibres discharging at rates which vary cyclically with respiration. The two components are more obvious when heard from the loudspeaker than in photographic records. In some fibres the maximum discharge rate occurs early in inspiration, and in others during expiration. The inspiratory fibres become dominant during dyspnoea. This feature in the main trunk of the superior laryngeal nerve of the dyspnoeic rabbit has been described by Petitpierre (1943). The cyclical discharge is not stopped by bilateral section of the recurrent laryngeal nerves nor does it depend to more than a small amount on the movements of air through the larynx. The cyclical component only ceases when the larynx is isolated from movements transmitted to it from adjacent structures. This confirms the findings of Petitpierre (1943)

in the rabbit. As has been mentioned earlier in this paper, there is no cyclical component in the outflow from the isolated larynx preparation. The activity in branch 1 from the *in situ* and the isolated preparations are shown together in Text-fig. 9. Only a part of the activity in branch 1 originates from the joint, and one of the difficulties in these experiments was to be reasonably certain that the receptors under observation were functionally part of the

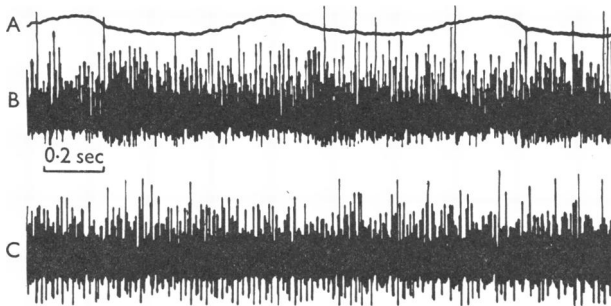


Text-fig. 7. Records from a filament of branch 1 of an isolated larynx preparation. (a) and (b) show the activity of three type 1 endings during rapid extension movements from full flexion to three-quarter extension. In record (a) some recruitment is shown, but in (b) the three endings begin to discharge almost simultaneously.



Text-fig. 8. Graph prepared from the preparation illustrated in Text-fig. 7 to show the adaptation of the sensory ending while the joint is motionless following the rapid extension movement. The impulses were counted in  $\frac{1}{4}$  sec periods.

joint. For this reason the preparation of a large number of single fibre dissections from branch 1 was not resorted to: though this method is of great value when a purely articular nerve is being examined. It was found to be more rewarding to study the activity in the intra-laryngeal branches of branch 1, where the destination of the fibres was more certain. Some fibres were found in branch 1 which appeared to be connected to slowly adapting endings stimulated by expiration, possibly by the bulging of some part of the glottis. Aldaya (1936) noted an augmentation in the discharge in the main trunk of the superior laryngeal nerve of the rabbit when air was blown through the larynx from a cannula in the trachea, and concluded that there were endings present which were stimulated by distension of the laryngeal cavity.

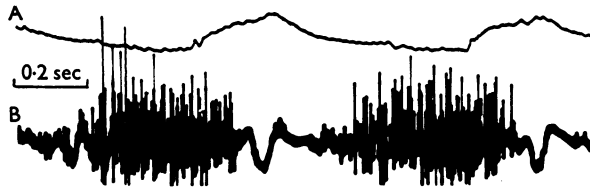


Text-fig. 9. A, the respiratory movements of the anaesthetized animal during eupnoea. B, the sensory outflow in branch 1. As will be seen there was only a slight change in the volume of sensory nerve impulses during the respiratory cycle. C, the sensory outflow from branch 1 of an isolated larynx preparation. Elevation of the respiration signal indicates inspiration.

*Activity in the intralaryngeal branches of branch 1.* Branch 1 passes through the inferior constrictor muscle and penetrates the thyroid cartilage. It then gives off two or three slender filaments, but during quiet breathing there is little activity in these. During swallowing movements a short outburst of sensory impulses occurs. Fibres are present which serve touch endings in the mucosa over the arytenoid cartilages and slowly adapting tension endings, but the site of the latter was not discovered. Slender branches are then given off to the aryepiglottic folds; these innervate touch endings and taste buds in the mucosa of the folds and there was some evidence that stretch-sensitive endings are present also.

A small branch is then given off to the joint and the remainder of the fibres form a bundle which passes between the dorsal mucosa of the epiglottis and the cartilage. This bundle serves the dense sensory innervation of the dorsal mucosa but may contain recurrent fibres to endings on the connective tissue band which links the cuneiform cartilage to the epiglottis. The small branch to the joint contains most of the proprioceptor fibres.

*The action of the epiglottic muscle.* This muscle, which is the functional equivalent of the hyoepiglottic muscle, contracts rhythmically with respiration. The contraction phase occurs during the early part of inspiration; in certain types of respiration it may begin to contract before expiration is complete. The anatomy of the epiglottic and hyoepiglottic muscles (supplied by the hypoglossal nerve) is described by Negus (1949, p. 136) and Sisson & Grossman (1950). Text-fig. 10 shows a recording of the electromyogram of the epiglottic muscle together with the respiratory movements of the xiphisternal region. The contraction of the muscle tends to extend the joint but the movement which occurs is usually small, as the ventral surface of the epiglottis is pressed against the soft palate. It is convenient to regard the epiglottis as a hinged lid over the orifice of the buccal cavity. When the epiglottic muscle contracts the lid is closed more firmly. A clue to the purpose of this contraction was provided in an experiment in which the muscle was detached

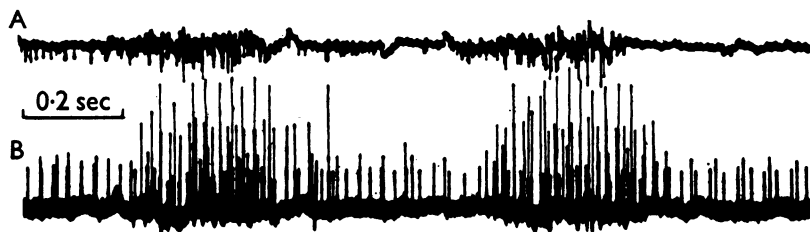


Text-fig. 10. Recordings to show the time relationship between the contraction of the epiglottic muscle and the respiratory movements. A, respiration indicator, ascent of the line indicates inspiration. B, the electromyogram of the epiglottic muscle. It will be seen that the muscle contracts before and during inspiration.

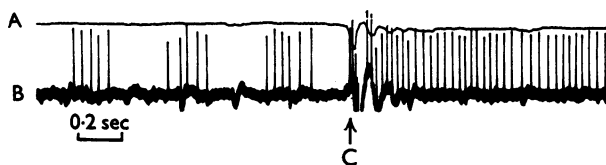
from the epiglottis and the ventral surface of the latter observed through a window cut in the mandible. It was then seen that during inspiration the epiglottis lost contact with the soft palate and allowed air to enter the pharynx through the mouth. This does not normally occur. The opening (flexion) was presumably caused by the lowered air pressure in the pharynx during inspiration. During dyspnoea the contraction of the muscle is increased in vigour and, of course, acts against an increased tendency for the epiglottic lid to be pushed open.

*The effect of contraction of the epiglottic muscle on the joint proprioceptors.* Since contraction of the muscle causes extension of the joint it is to be expected that it will initiate or increase the discharge of type 1 receptors and alter the frequency of type 2 receptors. Simultaneous recordings were made of the electromyogram of the epiglottic muscle and nerve action potentials in filaments dissected from branch 1. An example of this is given in Text-fig. 11, and it will be seen that two sensory units discharged only during the contraction of the muscle (one at 40 imp./sec and the other at 50–60 imp./sec). Two other units discharged continuously throughout but the frequency of one is raised

during the contraction period from 20 to about 100 imp./sec and the effect on the other is obscured. To ensure that these effects were correctly attributed to the epiglottic muscle another type of experiment was performed. Both the recurrent laryngeal nerves were cut and a thread tied to the tendon of the epiglottic muscle but without detaching it from the epiglottis. The movements



Text-fig. 11. A, electromyogram of the epiglottic muscle. B, nerve action potentials in a small filament of branch 1. There are four active proprioceptor fibres present. Two of these discharge during the contraction of the muscle, the other two discharge throughout the record. The frequency of one of the continuously discharging fibres rises during the contraction phase, the effect on the other is obscured.



Text-fig. 12. A, indicates the position of a thread attached to the tendon of the epiglottic muscle. Descent of the line indicates joint extension. A tension of 2 g was applied at point C. B, nerve impulses in a single fibre preparation from branch 1. The three impulse trains corresponded to the contraction of the epiglottic muscle. When the tension was applied at point C to simulate a sustained contraction of the muscle the trains were replaced by a slowly adapting discharge.

of the thread were picked up with a piezo crystal device. A single fibre preparation bearing trains of impulses synchronized to the contraction of the epiglottic muscle was dissected out. Text-fig. 12 shows three such trains of 5 and 6 impulses. A tension of 2 g was applied to the thread so as to simulate a sustained contraction of the muscle. It will be seen that the impulse trains were immediately replaced by a slowly adapting discharge; the frequency after 1 sec was 30 imp./sec.

#### *Histological results*

The three zones which by functional tests had been found to contain stretch receptors were examined histologically. In each case myelinated fibres were found to end on connective tissue. The form of the endings depended on the site.

*Endings on the perichondrium of the cuneiform cartilage.* The fibre usually broke up once or twice into short myelinated limbs, and these after a final node gave rise to a small zone of inter-connected plates and varicosities of neuroplasm. These plates were applied to the perichondrium. The ending is illustrated in Pl. 1, fig. 2.

*Endings in the aryepiglottic ligament.* The parent fibre usually broke up once or twice close to the ligament and the short myelinated limbs formed gave rise to a number of very fine non-myelinated fibres which penetrated into the crevices between the parallel connective tissue fibres of the ligament. The fibres usually appeared wavy or coiled. This ending is illustrated in Pl. 1, fig. 1.

*Endings in the connective tissue band between the cuneiform and epiglottic cartilages.* These were difficult to see because of the dense innervation of the overlying mucosa. No acceptable photographs were obtained. Where they were visible they resembled the endings in the aryepiglottic ligament.

#### DISCUSSION

Since previous electrophysiological work on joint proprioception has been centred on the knee joint, it is of interest to find a functionally similar sensory ending in what is anatomically a very different articulation. The functional properties of the laryngeal ending, as disclosed by the admittedly unstandardized stimuli used in this work, have the characteristic features of the knee-joint endings, namely they cease to discharge abruptly if the frequency falls to about 10 imp./sec, but above this frequency their adaptation rate is slow and they are capable of discharging regularly spaced impulses over long periods of time. They are sensitive to the stretching of the tissue on, or in which they are mounted, and can discharge when powerfully stimulated at more than 200 imp./sec. They are very sensitive to direct mechanical stimulation, as is produced when the site of the endings is probed. Gardner (1944) reported the sensitivity of the endings in the posterior capsule of the cat's knee joint to localized pressure.

With these properties in mind, it seems unlikely that the slowly adapting endings of the cat's toe, originally described by Adrian & Umrath (1929) and recently re-examined by Gray & Matthews (1951) are in the same category. The latter authors show records of an ending discharging irregularly at 3 imp./sec and found it relatively insensitive to direct mechanical stimulation. Indeed it is doubtful if sensitivity to joint movement or position is more than accidental since Adrian & Umrath (1929) reported that when the toe was put in a position of extreme flexion or extension and held there, occasional impulses continued to be discharged for a few seconds but eventually all activity ceased. This suggests that the ending, which is slowly adapting, had been subjected to a transient stimulation. One of the features of the knee- and

laryngeal-joint proprioceptors is that they are mounted on anatomical structures whose mechanical distortion depends on joint position, i.e. if the joint is motionless the distortion of the structure is unchanging too.

The use of the isolated preparation settled many difficulties. In earlier experiments it was not possible to decide the roles played by the extrinsic and intrinsic muscles, or indeed whether some of the active fibres observed in the superior laryngeal nerve did not, in fact, arise in the extrinsic muscles. The fact that proprioceptive discharge patterns could be obtained from the isolated joint which were similar to those obtained from the *in situ* preparation was regarded as good evidence that the essential proprioceptive mechanism lay in the joint region. Also, since most of the isolated preparations came from the corpses of animals not injected with urethane, the anaesthetic could have had little influence.

The observation that the proprioceptors were stretch-sensitive endings mounted on connective tissue elements differentially distorted by joint movement, e.g. during flexion the cuneiform system is relaxed and the aryepiglottic ligament is stretched, is paralleled by the observation that sensory elements are situated on the medial ligament of the knee (which is stretched during extension) and the observation of Boyd & Roberts (1953) of a nerve preparation containing two active fibres, one of which increased in frequency whilst the other decreased in frequency during a joint movement. Whether it will be possible to make a mechanical analysis of the distortion which occurs in such an organ as the posterior capsule of the knee is conjectural.

The dispersal of the thresholds of the proprioceptors is well shown in records both from the isolated and *in situ* preparation. The distribution of arcs of joint position over which individual endings are sensitive may be of no significance but it is easy to see how such an arrangement could be the basis of a system signalling joint position with great accuracy. It is not difficult to find reasons why an accurate proprioceptive system is required at this particular joint. The function of the epiglottis is much more restricted in man than in the rat. In a large number of mammals the epiglottis can seal the pharyngeal end of the mouth cavity either by contact with the buccal surface of the soft palate as in the dog or with the nasopharyngeal surface as in the present instance. Negus (1949, pp. 18-29) has made a study of the comparative anatomy and physiology of the epiglottis, and concludes that preservation of the sense of smell is the probable reason for the mouth-sealing function of the epiglottis. Presumably the rat can smell inspired air without interference from odours from material in the mouth, and the whole of the tidal air is passed through the nose. In this case the epiglottal taste-buds on the dorsal surface will be accessible to sapid materials in the inspired air. During respiration the epiglottal lid is kept closed, and any sliding movements between it and the soft palate will be signalled by rapidly adapting touch

receptors in the mucous membranes. It seems likely that the muscular effort required to keep the lid closed against pressure differences between the pharynx and mouth will vary under different conditions, and a proprioceptive mechanism would be necessary at the joint to provide an effective control over the muscles acting on the larynx. During swallowing the lid opens and the movement must be co-ordinated with the large number of rapid muscular adjustments which comprise the act. An attractive opportunity exists to test some of the foregoing speculation since it should be possible to establish experimentally whether the joint proprioceptors influence the outflow to the epiglottic and other muscles which contract regularly with respiration in the anaesthetized animal.

The histological findings support the idea that the form of the slowly adapting stretch receptor depends on the nature of the tissue in which it is embedded. A rather similar conclusion was reached in the case of the knee-joint endings (Andrew, 1954*a*). When the ending lay against the dense tissue of the perichondrium of the cuneiform cartilage it took the form of closely applied plates of neuroplasm and resembled the Golgi tendon ending. When the ending lay on the aryepiglottic ligament it was able to penetrate as fine non-myelinated fibres into the crevices between the connective tissue fibres of the ligament.

#### SUMMARY

1. Afferent discharges were recorded from proprioceptors located at the thyroepiglottic joint of the rat.

2. An isolated larynx preparation was used to study the responses to position and passive movement. The responses to movements produced by muscular action were recorded from the anaesthetized animal.

3. The proprioceptors were found to be slowly adapting stretch receptors but they were mounted on tissues that were differentially stretched during flexion and extension. Consequent to this, two types of response were recognized, one to extension only and the other to a deviation either towards extension or flexion from a mid-position. Locations for the endings responsible for the two types of response were suggested.

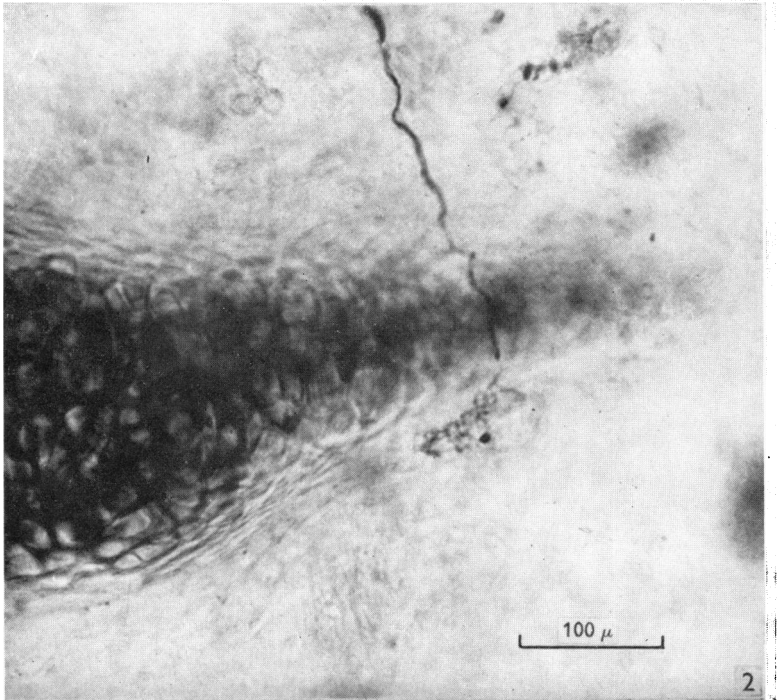
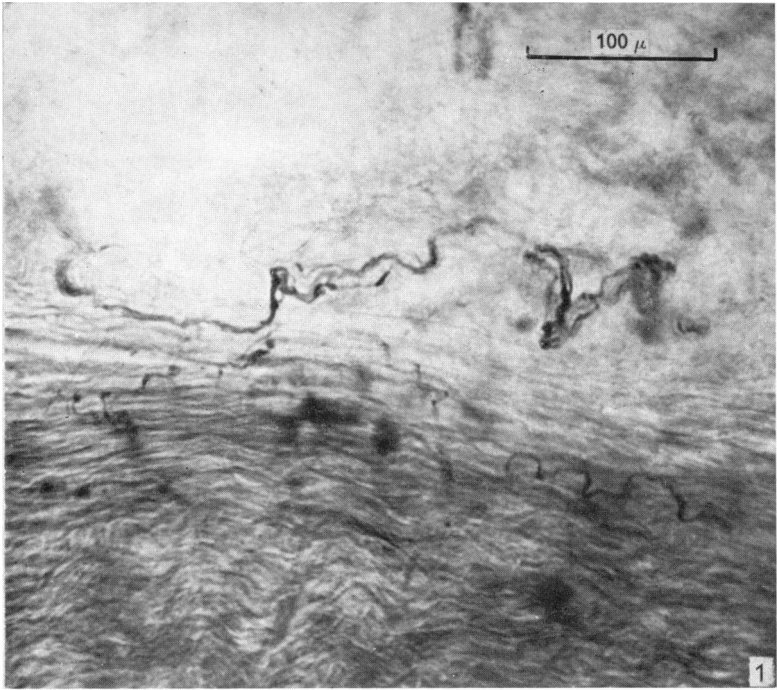
4. It was considered that the proprioceptors could give enough information for a central mechanism to gauge accurately the position and movement of the epiglottis.

5. The laryngeal-joint proprioceptors were found to be similar in many respects to the previously described proprioceptors of the knee joint.

6. Structures found to be stretch-sensitive were examined histologically with methylene blue. Nerve endings on connective tissue were found; the form of the ending appeared to depend on the type of connective tissue.

I wish to thank Prof. G. H. Bell for his interest in this work.





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## EXPLANATION OF PLATE

Both preparations were stained with methylene blue.

- Fig. 1. Nerve ending amongst the fibres of the aryepiglottic ligament. The connective tissue fibres of the ligament can be seen as wavy horizontal lines in the lower half of the photograph. The myelinated parent fibre has a final, darkly stained, node, close to the border of the ligament and then gives rise to very fine non-myelinated fibres which penetrate between the connective tissue of the ligament. These can be seen in a roughly coiled form.
- Fig. 2. Nerve ending on the perichondrium of the cuneiform cartilage. The perichondrial cells are almost transparent but the matrix of the cartilage appears dark. The ending is in the form of interconnected plates and granules of neuroplasm attached to the terminal node of the myelinated parent fibre. The ending zone of another branch (very much out of focus) may be seen as a shadow in the top right corner of the photograph.