*Journal of Physiology* (1989), **410**, *pp*. 35–44
*With 3 text-figures*
*Printed in Great Britain*



# DISTRIBUTION OF MESENCEPHALIC NUCLEUS AND TRIGEMINAL GANGLION MECHANORECEPTORS IN THE PERIODONTAL LIGAMENT OF THE CAT

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(*Received 3 June 1988*)

## SUMMARY

1. In anaesthetized cats recordings have been made in the mesencephalic nucleus of the fifth cranial nerve and the trigeminal ganglion from neurones that respond when forces are applied to the mandibular canine tooth. The site of the mechanoreceptors in the periodontal ligament and their distribution around the tooth root have been determined.

2. Receptors with their cell bodies in the mesencephalic nucleus were found to be situated in the periodontal ligament in a discrete area intermediate between the fulcrum and apex of the tooth, while those in the trigeminal ganglion were situated in the whole area of the periodontal ligament between the fulcrum and apex of the tooth.

3. All of the located mechanoreceptors responded maximally when that part of the ligament in which they lay was put under tension.

4. The directional sensitivities of the mechanoreceptors suggested that there was an uneven distribution around the tooth root of receptors with cell bodies in the mesencephalic nucleus. In contrast mechanoreceptors with cell bodies in the trigeminal ganglion were distributed more equally around the tooth root. The rationale for the differences requires further investigation.

## INTRODUCTION

When a force is applied to a tooth mechanoreceptors in the periodontium are stimulated. The receptors may be situated in any of the tissues that comprise the periodontium, i.e. gingiva, cementum, periodontal ligament and the alveolus (British Standards, 1983) and have loosely been described as 'periodontal mechanoreceptors' (for reviews see Hannam, 1982; Linden, 1989). Electrophysiological studies have demonstrated that the cell bodies of these mechanoreceptors are found in two anatomically distinct sites: the mesencephalic nucleus of the fifth cranial nerve (Corbin & Harrison, 1940; Jerge, 1963; Cody, Lee & Taylor, 1972; Linden, 1978; Amano & Iwasaki, 1982; Cash & Linden, 1982*a*; Passatore & Filippi, 1983; Passatore, Lucchi, Filippi, Manni & Bortolami, 1983) and the trigeminal ganglion (Kerr & Lysak, 1964; Beaudreau & Jerge, 1968; Mei, Hartmann & Roubien, 1970, 1975; Appenteng, Lund & Seguin, 1982; Cash & Linden, 1982*a*). However, in all of these studies the precise locations of the receptors were not determined; they could have been situated in any of the tissues in the periodontium.

In a peripheral recording study (Cash & Linden, 1982*b*) mechanoreceptors were located in the periodontal ligament itself. They were situated in the whole area of the ligament between the fulcrum and the apex of the tooth. Observations on the response of the mechanoreceptors to a force applied to the crown of the tooth in the direction of maximum sensitivity suggested that they responded when that part of the ligament in which they lay was put under tension. It was also suggested that the mechanoreceptors were distributed equally around the tooth root. However, it was not known whether the cell bodies of the mechanoreceptors were in either the mesencephalic nucleus or the trigeminal ganglion. Anatomical studies in the cat (Weill, Bensadoun & de Tourniel, 1975; Chiego, Bradley, Cox & Avery, 1979; Byers & Matthews, 1981; Gottlieb, Taylor & Bosley, 1984; Byers, O'Connor, Martin & Dong, 1986) have shown neurones to be present in the periodontal ligament which have their cell bodies in either the trigeminal ganglion or the mesencephalic nucleus. However, a clear understanding of the position and distribution of the receptors themselves has not yet emerged.

The purpose of the present study was to determine whether there is a difference in the distribution of the mechanoreceptors in the periodontal ligament with their cell bodies in the mesencephalic nucleus to those with their cell bodies in the trigeminal ganglion. Some of the results have already been reported in a preliminary form (Linden & Scott, 1987, 1988*a*, *b*).

## METHODS

Anaesthesia was induced in twenty-four adult cats of weight 2·2–5·2 kg with ketamine hydrochloride (22 mg $kg^{-1}$) and maintained with $\alpha$-chloralose (initial loading dose, 50 mg $kg^{-1}$; continuous infusion, between 4·6 and 23 mg $h^{-1}$). The animals were artificially ventilated through a tracheostomy tube with moistened 40 % oxygen in air using a modified Ideal Starling pump. End-tidal carbon dioxide was maintained between 3·5 and 4·5 %. The body temperature was maintained at $37 \pm 0{\cdot}2$ °C with a thermostatically controlled electric blanket using feed-back from a rectal thermistor probe. Throughout all of the experiments the mean arterial blood pressure was above 10 kPa.

Silver-wire stimulating electrodes were placed in contact with the inferior alveolar nerve in all experiments where recordings were made in the mesencephalic nucleus and a number of experiments where recordings were made in the trigeminal ganglion. The bone overlying the labial and mesiolabial aspect of the left mandibular canine tooth root was pared away using the technique described in Cash & Linden (1982*b*). The extent of the bone paring is shown in Fig. 1. The jaws were immobilized by using acrylic blocks cemented between the maxillary and mandibular molar teeth.

The head of the cat was placed in a stereotaxic frame and positioned in a standard stereotaxic position using infraorbital bars. Extracellular recordings were made using glass-insulated, gold- and platinum-black-coated tungsten microelectrodes (tip length, 15–20 $\mu$m; impedance, 50 kΩ to 1 MΩ at 1 kHz; Merrill & Ainsworth, 1972) inserted into either the mesencephalic nucleus or the trigeminal ganglion. The whole of the accessible region of the left mesencephalic nucleus was explored (A4–P4, 2·3 mm lateral to mid-line; Berman, 1968) while giving square-wave pulses (5–8 V, 0·1 ms duration, 1 Hz) to the inferior alveolar nerve. The left trigeminal ganglion was explored by direct vision. Output from the recording electrodes was amplified through an AC preamplifier and amplifier (Neurolog), and recorded on FM tape. The data were displayed on oscilloscopes and by a high-speed signal store (Grafitek UK) on a BBC microcomputer.

The site of the mechanoreceptors in the pared-away aspect of the periodontal ligament and the position of the fulcrum of the tooth were determined using procedures described by Cash & Linden (1982*b*). The direction of maximum sensitivity of the located and unlocated mechanoreceptors was determined by applying forces with a pair of watch-spring forceps to the tip of the crown of the mandibular canine tooth in eight directions at 45 deg intervals. Observations were made on the

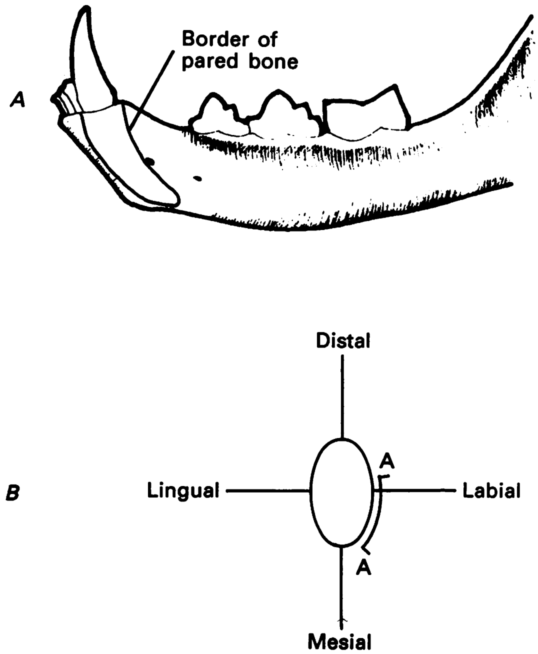


Fig. 1. Diagrams to show the area overlying the labial and mesiolabial aspect of the periodontal ligament in which bone was pared away. The receptors could be stimulated in the periodontal ligament through a very thin layer of bone by punctate and electrical stimulation. *A*, a lateral view of the mandible to show the area of bone paring; *B*, a transverse section through the tooth root to show the area of bone paring which is indicated by the line AA.

adaptation of receptors to a force applied to the crown of the tooth and the conduction velocities of the located mechanoreceptor neurones were also determined.

## RESULTS

The criteria used for locating a mechanoreceptor in the periodontal ligament were that action potentials of the same size and shape were recorded when (a) the tooth was mechanically stimulated, (b) a small area of periodontal ligament was mechanically stimulated and (c) an identical area of periodontal ligament as in (b) was electrically stimulated. These criteria have been described fully by Cash & Linden (1982*b*). In eleven cats in which recordings were made in the mesencephalic nucleus forty-three mechanoreceptors were found which responded to mechanical stimulation of the mandibular canine tooth. Of these, thirteen mechanoreceptors were located in the pared-away part of the periodontal ligament. The mechanoreceptors were situated between the fulcrum and the apex of the tooth but were not evenly distributed between the two sites. They were all found to be positioned in an area of the ligament which was intermediate (but not midway) between the fulcrum and the apex of the tooth. No mechanoreceptors were found very close to the fulcrum or above the fulcrum nor were they found in the lower part of the ligament closer to the apex of the tooth. Their positions in the periodontal ligament are shown in Fig. 2*A*.

In eleven cats in which recordings were made in the trigeminal ganglion 104 mechanoreceptors were found of which seventeen were located in the pared-away part of the periodontal ligament. The mechanoreceptors were found in the whole area of the ligament from the fulcrum to the apex of the tooth and they were more evenly distributed than those located when recording in the mesencephalic nucleus. None were found above the fulcrum of the tooth. Overall the mechanoreceptors were spread over a much wider area of the periodontal ligament than those located when recording in the mesencephalic nucleus; many were found in the lower part of the ligament closer to the apex of the tooth and some were found very close to the fulcrum. The variance in the position of the trigeminal ganglion mechanoreceptors in the ligament was significantly greater than the variance of the mesencephalic mechanoreceptors ($P < 0{\cdot}001$, two-tailed, $F$ test). Their positions in the periodontal ligament are shown in Fig. 2*B*.

All mechanoreceptors showed a direction of maximum sensitivity to a force applied to the crown of the tooth. It was very easy to observe a direction of stimulation that caused the greatest discharge of a mechanoreceptor. In all experiments the located mechanoreceptors in the labial and mesiolabial aspect of the ligament responded maximally to a force applied to the lingual or distolingual surface of the crown.

In experiments in which recordings were made in the mesencephalic nucleus the direction of maximum sensitivity of all receptors, both located and unlocated, to a force applied to the crown of the tooth, was recorded in all eleven cats where bone paring was performed and for an additional eight receptors in two cats in which bone paring was not performed. It was found that there was an uneven distribution of the mechanoreceptors around the root of the tooth; the majority (70·6%) had their direction of maximum sensitivity when a force was applied in an area extending from the lingual to the distal surface of the crown. A much smaller number of mechanoreceptors was found which responded maximally to a force to other surfaces of the tooth crown ($\chi^2$ test, $P < 0{\cdot}001$). In contrast, in experiments in which recordings were made in the trigeminal ganglion, the directions of maximum sensitivity of the 104 mechanoreceptors were equally distributed around the tooth root ($P > 0{\cdot}1$). Figure 3*A* and *B* shows the direction of maximum sensitivity for all of the mechanoreceptors recorded in this study.

When recording in the mesencephalic nucleus it was found that both the located and unlocated receptors adapted out within a few seconds when a force was applied to the crown of the tooth. No very slowly adapting mechanoreceptors were observed. However, when recording in the trigeminal ganglion a large number of the mechanoreceptors, both located and unlocated, were found to have slowly adapting properties in that they did not adapt out to a prolonged force applied to the crown of the tooth. Mechanoreceptors were also found which adapted within a few seconds,

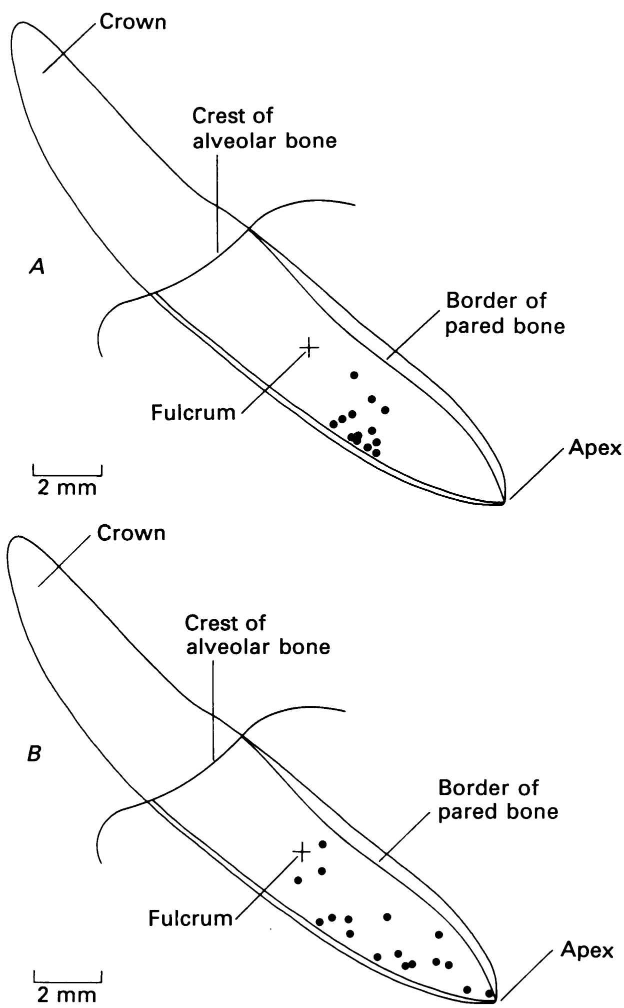


Fig. 2. Diagram to show the position of the located receptors relative to the fulcrum of the mandibular canine tooth in the pared-away part of the periodontal ligament. *A*, when recordings were made in the mesencephalic nucleus; *B*, when recordings were made in the trigeminal ganglion. The mean length of the tooth root was 11·1 mm (S.D. $\pm$ 1·1) and the mean length from the crest of the alveolar bone to the fulcrum of the tooth was 3·8 mm (S.D. $\pm$ 0·5).

similar to those found when recording in the mesencephalic nucleus. In addition a few rapidly adapting receptors which gave only one or two impulses to a force applied to the crown of the tooth were observed.

The conduction velocities of the located neurones were determined from stimulation at the receptor site in the periodontal ligament. There was no significant difference in the conduction velocity of the thirteen located mechanoreceptor neurones (mean $\pm$ S.D., $33 \pm 7$ m $s^{-1}$) recorded in the mesencephalic nucleus to the seventeen located mechanoreceptor neurones (mean $\pm$ S.D., $40 \pm 10$ m $s^{-1}$) recorded in the trigeminal ganglion ($P > 0{\cdot}05$, two-tailed, Mann–Whitney test). In addition the

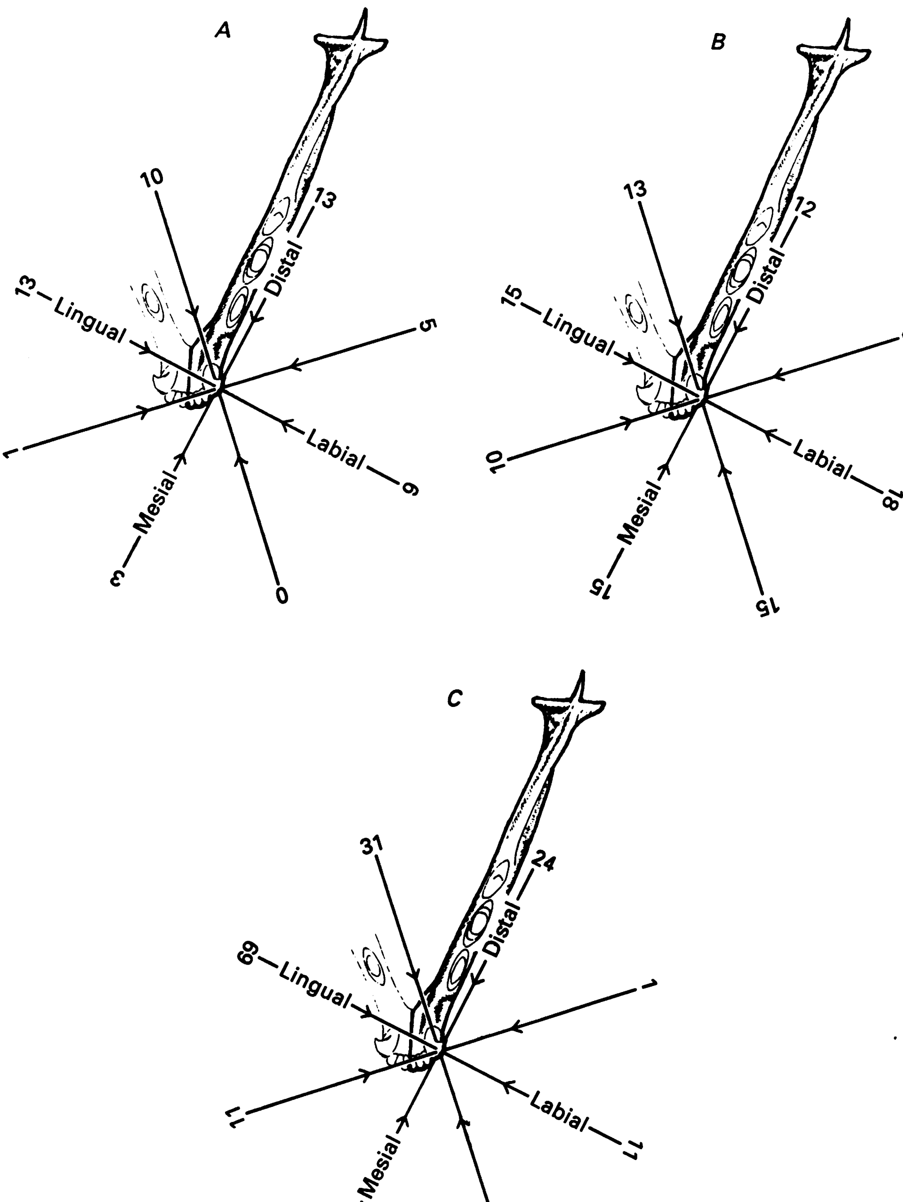


Fig. 3. Plan views of the left mandible to show the directions of maximum sensitivity of the mechanoreceptors which responded to a force applied to the left mandibular canine tooth. The numbers denote the sum of the mechanoreceptors with the direction of maximum sensitivity in each of the eight directions: *A*, when recordings were made in the mesencephalic nucleus ($n = 51$); *B*, when recordings were made in the trigeminal ganglion ($n = 104$); *C*, when recordings were made in the mesencephalic nucleus in an earlier study by Linden (1978) in which no previous analysis had been made ($n = 157$).

conduction velocities of the located neurones when recording in the mesencephalic nucleus were found to be significantly greater when stimulating through the electrodes in contact with the inferior alveolar nerve (mean ± S.D., 47 ± 9 m $s^{-1}$) than when stimulating at the receptor site ($P < 0{\cdot}002$, two-tailed, Mann–Whitney test). It was not possible to do this in experiments in which recordings were made in the trigeminal ganglion because when the inferior alveolar nerve was stimulated a compound action potential was recorded at the trigeminal ganglion and it was not possible to distinguish the response of the single periodontal ligament mechanoreceptor neurone which had been located.

## DISCUSSION

It was possible to locate the sites of mechanoreceptors in the periodontal ligament of the mandibular canine tooth when recordings were made in the mesencephalic nucleus and the trigeminal ganglion. However, there were differences in the distribution of the mesencephalic nucleus mechanoreceptors compared with the trigeminal ganglion mechanoreceptors.

When recordings were made in the mesencephalic nucleus the mechanoreceptors were located in a discrete area of the periodontal ligament between the fulcrum and the apex of the tooth. In an autoradiographic study (Byers *et al.* 1986) published while the present work was in progress tritiated proline was injected into the mesencephalic nucleus of the cat. Labelled structures including putative nerve endings were found in the periodontal ligament in the area close to the root apex, which is in contrast to the present study in which no mechanoreceptors were located in the apical part of the ligament. The different findings of the two studies are difficult to resolve at present.

In contrast when recordings were made in the trigeminal ganglion mechanoreceptors were distributed over a much wider area of the periodontal ligament. Anatomical studies in the cat (Weill *et al.* 1975; Byers & Matthews, 1981) have shown labelled neurones in the periodontal ligament following the injection of tritiated amino acids into the trigeminal ganglion. However, in the present study it has been possible to determine by direct stimulation the sites of the mechanoreceptors themselves.

In all experiments, the located receptors in the periodontal ligament, were below the fulcrum of the tooth. Since the tooth rotates about its fulcrum when a force is applied to the crown of the tooth the directional sensitivities of the located receptors suggest that they respond when that part of the ligament in which they lie is placed under tension. This confirms the findings of Cash & Linden (1982*b*).

When recordings were made in the mesencephalic nucleus the directions of maximum sensitivity of the mechanoreceptors were unequally distributed around the tooth root. Since the majority of neurones recorded responded maximally when a force was applied to the area extending from the lingual to the distal surface of the crown and the tooth rotates about its fulcrum, this would indicate that the majority of receptors lie in an area extending from the labial to the mesial aspect of the periodontal ligament. These observations are further reinforced by a retrospective examination of data collected in a study by Linden (1978). Recording in the mesencephalic nucleus the direction of maximum sensitivity of 157 mechanoreceptors which responded to a force applied to the mandibular canine tooth had been observed but a comparison of them had not been made. The technique for location of mechanoreceptors within the periodontal ligament had not been developed at this time and the observation that the mechanoreceptors responded when the ligament was under tension had not been made. It was found on re-examination of the data that the majority of the mandibular canine mechanoreceptors (79·0%) responded maximally when a force was applied to the same area of the crown of the tooth as in the present series of experiments. These retrospective data are shown in Fig. 3*C* and reinforce considerably the results found from the smaller sample of receptors in the present study.

In the present experiments mechanoreceptor neurones were identified in the mesencephalic nucleus by electrical stimulation of the inferior alveolar nerve. There is no evidence that the uneven distribution could be explained by other neurones innervating the periodontal ligament through a different nerve. The only possible one could be the lingual nerve. However, Corbin (1940) found no evidence of degeneration in the lingual nerve following lesions to the mesencephalic nucleus whereas degeneration was observed in the inferior alveolar nerve. Furthermore, in this study and in a previous study (Linden, 1978) all receptors that responded to mechanical stimulation of the mandibular canine tooth also responded to electrical stimulation of the inferior alveolar nerve.

When recordings were made in the trigeminal ganglion the distribution of the directions of maximum sensitivity of the mechanoreceptors to a force applied to the tooth indicated that there was no predominant directional sensitivity. This suggests these mechanoreceptors are distributed in the periodontal ligament much more evenly around the tooth root.

Many more mechanoreceptors which responded to mechanical stimulation of the canine tooth were found when recordings were made in the trigeminal ganglion compared to recordings made in the mesencephalic nucleus. This may be due to the fact that there is a greater representation of periodontal ligament mechanoreceptors in the trigeminal ganglion than in the mesencephalic nucleus but it could also be due to the ease of which it was possible to record from the two anatomically distinct sites. In a peripheral study Cash & Linden (1982*b*) suggested that the mechanoreceptors in the periodontal ligament were equally distributed around the mandibular canine tooth root. The relative contribution of both mesencephalic and trigeminal ganglion mechanoreceptors to the overall distribution in the periodontal ligament therefore requires further study.

When recordings were made in the mesencephalic nucleus it was found that no very slowly adapting mechanoreceptors were present. This is in agreement with the studies of Jerge (1963) and Linden (1978). However, when recordings were made in the trigeminal ganglion the mechanoreceptors had a range of adaptation properties from rapidly to very slowly adapting which is also in agreement with previous studies (Kerr & Lysak, 1964; Beaudreau & Jerge, 1968). The position of the mechanoreceptors in the present study and the observations on adaptation are in accord with observations made on the response characteristics of receptors in peripheral studies by Linden & Millar (1988). There was no difference in the conduction velocities of located mechanoreceptor neurones when recording in either the mesencephalic nucleus or the trigeminal ganglion. When recording in the mesencephalic nucleus, the conduction velocity of neurones when the inferior alveolar nerve was stimulated was greater than when the receptor site was stimulated. This is likely to be due to narrowing of the axon and myelin sheath in the terminal part of the neurone (Halata & Munger, 1985). However, it could also be due in part to the lower temperature as the action potential travels through the exposed part of the ligament (Franz & Iggo, 1968).

In conclusion there are differences in the distribution within the periodontal ligament of the mandibular canine tooth of the mechanoreceptors with their cell bodies in the mesencephalic nucleus compared with those with their cell bodies in the trigeminal ganglion. The rationale for these differences is not yet known. Receptors in the periodontal ligament have been implicated to have a role in the control of activity of the muscles involved in mastication (reviewed in Matthews, 1975; Dubner, Sessle & Storey, 1978) and also in the control of salivation (Hector & Linden, 1987). It is possible that the mechanoreceptors with cell bodies in the mesencephalic nucleus have a different functional role to those with cell bodies in the trigeminal ganglion. This requires further study.

This study was supported by a grant from the Medical Research Council. We are indebted to R. Roberts for technical assistance, G. Randall for advice on the statistics and R. A. Wood for artwork.

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