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PROPERTIES OF INTRAORAL MECHANORECEPTORS REPRESENTED IN THE MESENCEPHALIC NUCLEUS OF THE FIFTH NERVE IN THE CAT

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SUMMARY

1. The activity of neurones in the mesencephalic nucleus of the fifth nerve that respond to forces applied to the teeth were recorded using extracellular microelectrodes; the properties of these neurones have been studied.

2. Electrophysiological evidence consistent with the view that primary afferent intraoral mechanoreceptor fibres have their cell bodies in the trigeminal mesencephalic nucleus is presented.

3. Two groups of intraoral mechanoreceptor neurones were found. The first group, the periodontal mechanoreceptor neurones, which have been described by previous workers, responded to electrical stimulation of the ipsilateral superior or inferior dental nerves and to forces applied to single teeth in the ipsilateral maxilla or mandible respectively. The response characteristics of the mesencephalic periodontal mechanoreceptor neurones differed in two respects from those observed in peripheral nerve studies by previous workers: (*a*) there were no spontaneously active neurones, and (*b*) there were no neurones that responded for over 10 sec to a sustained application of a suprathreshold mechanical stimulus to the teeth.

The second group, not described before, responded to electrical stimulation of the ipsilateral palatine nerve, and responded to forces applied to all the teeth in the maxillary arch, both contralateral and ipsilateral as well as to forces applied to the nose and hard palate. The site of these receptors is unknown. They have been termed 'Type P' intraoral mechanoreceptors.

4. The recording sites of both the periodontal and Type P mechanoreceptor neurones were all situated in the caudal part of the mesencephalic nucleus of the fifth nerve.

INTRODUCTION

Activity of receptors that respond to forces applied to the teeth and their supporting structures have been recorded from peripheral nerve fibres (for review see Anderson, Hannam & Matthews, 1970) and from cells in both the trigeminal Gasserian ganglion (Kerr & Lysak, 1964; Beaudreau & Jerge, 1968; Mei, Hartmann & Roubien, 1970, 1975) and the mesencephalic nucleus of the fifth nerve in the cat (Corbin & Harrison, 1940; Jerge, 1963; Cody, Lee & Taylor, 1972).

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The recordings from the mesencephalic nucleus have shown neurones that respond not only to stimulation of tooth mechanoreceptors but also to stimulation of jaw elevator muscle spindles.

Degeneration studies have demonstrated that many of the fibres in both the maxillary and mandibular division of the trigeminal nerve have their cell bodies in the mesencephalic nucleus (Corbin, 1940; Szentágothai, 1948). Although it is generally assumed that the neurones in the mesencephalic nucleus that respond to mechanical stimulation of the teeth are those of primary afferent fibres, and that they represent those fibres that showed degeneration after a lesion in the mesencephalic tract, there has been no critical testing of this assumption.

The aim of the present experiments was to attempt to confirm electrophysiologically that the neurones in the mesencephalic nucleus that respond to forces applied to the teeth are cell bodies of primary afferent fibres and to study their functional properties.

During this study a group of neurones with functional characteristics not previously described was found. A preliminary report on these neurones has previously been published (Linden, 1976).

METHODS

Forty adult cats, 2·0–3·5 kg in weight, anaesthetized with sodium pentobarbitone (initial dose not exceeding 45 mg.kg^{-1} I.P.; maintenance dose of 3 mg.kg^{-1} I.V.) were used. The cats were maintained at a light anaesthetic level, at which the flexion withdrawal reflex could just be elicited. An electric blanket was wrapped around the cat's body and the body core temperature was maintained thermostatically at 37 ± 0·02 °C using feed-back from a thermister probe inserted into the peritoneal cavity.

The left inferior dental nerve was exposed for about 1 cm at the lower border of the left side of the mandible, and carefully separated from the inferior dental artery; a small piece of paraffin wax was interposed between nerve and artery. For electrical stimulation and whole nerve recording, two silver wire (0·2 mm diameter) electrodes were placed about 3 mm apart around the intact nerve. The leads were fixed to the adjacent bone using self-curing dental acrylic (Simplex, Howmedica International Ltd) and the nerve and electrodes were then covered with wax (melting pt 40 °C). The whole area was then covered with the dental acrylic and the incision stitched up. The left superior dental nerve was exposed in the floor of the orbit by removing the left eye. Two small holes about 3 mm apart were drilled on the left side of the palate distal to the posterior palatine foramen and two silver electrodes were placed in contact with the left palatine nerve.

After positioning the head in a stereotaxic frame using the infraorbital and palatal bars to fix the cat in a standard stereotaxic position, a bar was cemented with the self-curing dental acrylic to two screws inserted into the superior wall of the frontal sinus of the cat's head. After the acrylic had set, the bar was bolted to the frame and the infraorbital and palatal bars removed, which facilitated access to the oral structures.

Glass insulated, platinum and iron plated, tungsten micro-electrodes (tip length 10–20 μm, impedance 50 kΩ–1 MΩ at 1 kHz) (Merrill & Ainsworth, 1972; Merrill, 1974) were directed caudally, at a 30° angle to the vertical, through a square hole (side 15 mm) in the left side of the cranium. The 30° angle allowed access to the more caudal regions of the nucleus that would normally be inaccessible from the middle cranial fossa due to the angled bony tentorium.

The whole of the accessible region of the mesencephalic nucleus on the left side of the cat was explored (Horsley-Clarke co-ordinates A4.0–P4.0, 2·3 mm lateral to the mid line, Berman 1969). The electrode tracks were placed about 200 μm apart.

During stimulation using the central micro-electrode, differential recordings were made from the silver wire electrodes in contact with the peripheral nerves. The responses were averaged over a number of stimuli using a signal averaging computer (Datalab DL. 4000) resulting in an improvement of the signal-to-noise ratio.

An isolated stimulator was used to apply single shock stimuli to the peripheral nerves with an intensity adequate to produce a jaw opening reflex (range 2–5 V, 20–200 μsec duration).

Mechanical stimulation of the intraoral structures was made either with a hand-held insulated metal rod, used primarily to determine the receptive field of neurones being recorded from centrally, or, for more quantitative measurements, with an electromechanical force generator (Pye Ling V47, 30 Ω). The force generator incorporated strain gauges to record the applied strain and was attached to the tooth with a small perspex cap so that it could be used to either push or pull a test tooth.

An isolated constant current stimulator was used to apply stimuli through the micro-electrode to the mesencephalic nucleus. Cathodal stimuli of between 1 and 10 μA and 20 μsec in duration were applied through the micro-electrodes whilst recording from the intact peripheral nerves. Iron was not released from the tip of the micro-electrodes with this polarity.

The orthodromic and antidromic conduction delays to electrical stimulation of the neurone peripherally or centrally were measured to the point of first deviation from the base line and no allowance was made for utilization time. At the end of an experiment the distance between the peripheral electrodes and central micro-electrode was measured using a piece of soft wire bent to follow the course of the nerve.

The recording sites of all the neurones were determined from their stereotaxic co-ordinates. No allowance was made for individual variation between cats, nor for the possibility of deviation of the electrodes when penetrating the cerebral hemispheres and brain stem.

For twenty-five of the neurones, iron was deposited at the recording site by passing an anodal current of 2 μA for 10–20 sec. At the end of the experiment the brain stem was removed and immersed in 1 % potassium ferrocyanide in 10 % formalin for over 2 days.

The specimens were embedded in celloidin and sectioned at 100 μm and stained with neutral red. The Prussian blue marks could be readily seen against the counterstain.

RESULTS

Whilst exploring the region of the midbrain containing the mesencephalic nucleus, the inferior dental, superior dental or the palatine nerve was electrically stimulated at 1 Hz with square pulses (range 2–5 V, 20–200 μsec duration).

Two types of unitary response were encountered in the region of the mesencephalic nucleus. The first was characterized by a single all-or-none short latency (approx. 2 msec) response to electrical stimulation. These neurones responded to mechanical stimulation of the teeth or surrounding structures but did not respond to jaw opening. The second type responded after a longer latency (over 10 msec) and the activity was related to jaw opening. These latter neurones did not respond to forces applied to the teeth or the surrounding structures. The first group were classified as intraoral mechanoreceptor neurones, and the second group, which were not investigated further in this study, were classified as jaw elevator muscle spindle neurones.

Activity from a total of 325 intraoral mechanoreceptor neurones was recorded. All neurones gave a single all-or-none response to a single electrical stimulus applied to either the superior dental, or the inferior dental or the palatine nerves (Fig. 1*A*). All were able to follow exactly trains of stimuli of over 100 Hz for periods of over 2 sec.

In all cases the action potentials evoked by mechanical stimulation of the tooth were identical in size and wave form to the one evoked by electrical stimulation of the peripheral nerve.

Forty-one intraoral mechanoreceptor neurones were electrically stimulated centrally and the response recorded at the peripheral electrodes. The latency for antidromic conduction was compared with that for orthodromic conduction. Stimuli of between 1 and 10 μA and 20 μsec in duration were applied through the

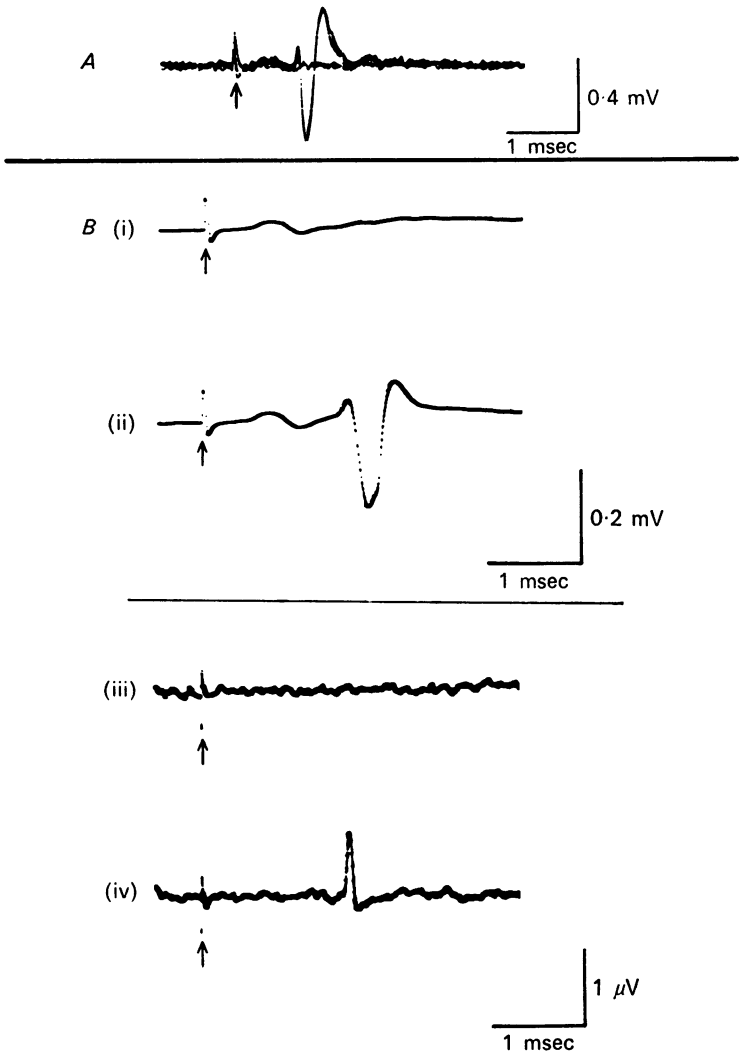

Fig. 1. *A*, an example of a single all-or-none response recorded from the mesencephalic nucleus during electrical stimulation of the superior dental nerve. Four consecutive traces were superimposed. The time at which stimuli were applied is marked by the arrow. The stimuli were 0·95, 1·0, 1·05 and 1·10 V (20 μsec duration). Stimuli up to 10 V gave no increase in the size or number of action potentials. The conduction distance was 58 mm. *B*, orthodromic and antidromic action potentials recorded from a single intra-oral mechanoreceptor neurone. Micro-electrode recordings from the mesencephalic nucleus during electrical stimulation of the inferior dental nerve (orthodromic) at (i) 0·70 V 20 μsec duration (no responses), (ii) 0·74 V 20 μsec duration (100 % responses), Whole nerve recordings from the inferior dental nerve during electrical stimulation via the micro-electrode in the mesencephalic nucleus (antidromic) at (iii) 4·0 μA 20 μsec duration (no responses), (iv) 5·0 μA 20 μsec duration (100 % responses). Each record is the average of 256 responses. The time at which the stimuli were applied is indicated by the arrows. The conduction distance was 65 mm.

micro-electrode. To improve the signal-to-noise ratio the responses were averaged over 256 stimuli (in all forty-one cases the response was just visible without averaging). Separate averages were made for a range of stimuli (1–10 μA). The stimulus was always delivered with the micro-electrode in a position for maximal orthodromic response. Movement of the micro-electrode vertically in either direction resulted in an increase stimulus strength needed to evoke a response recorded at the peripheral electrode. In all cases all-or-none activity was resolved for both orthodromic and antidromic conditions.

The antidromic conduction delays in each of the forty-one neurones studied were identical to the corresponding orthodromic delays between the same two electrodes. All the antidromic responses were able to follow stimulus frequencies of over 100 Hz for periods of over 2 sec. Fig. 1*B* shows examples of responses recorded centrally and peripherally using the same two electrodes. The earlier component occurring after about 0·5 msec was always present and is thought to represent the compound volley on passage to the brain stem and is to be contrasted with the all-or-none nature of the unitary event near the tip of the electrode.

The sizes of the action potentials recorded in the study range between 0·05 and 1·5 mV. The wave forms were triphasic (positive-negative-positive).

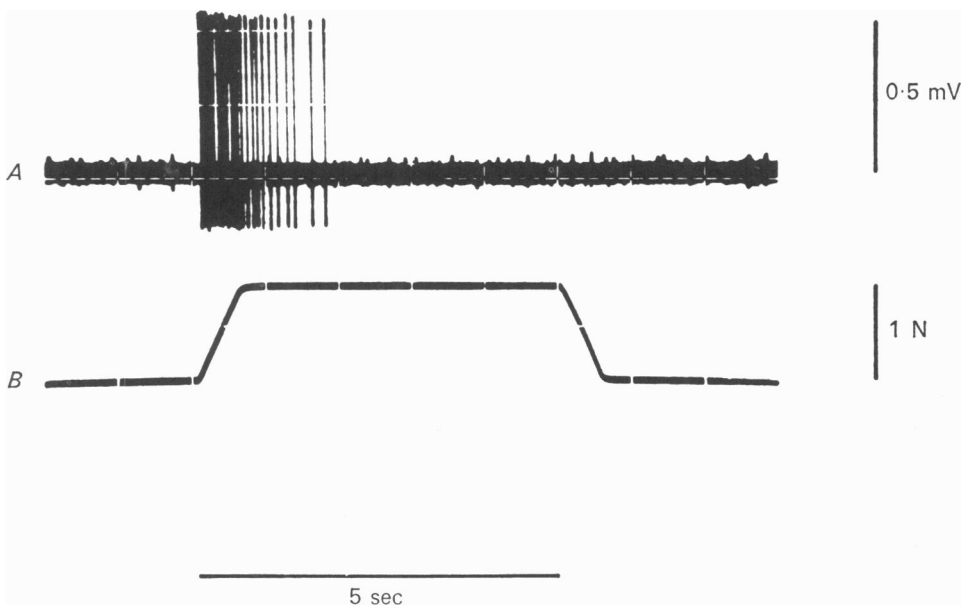

Fig. 2. The response at a mesencephalic recording electrode (*A*) of a periodontal mechanoreceptor neurone to a controlled force (*B*) applied to the mesial surface of the lower left canine.

Periodontal mechanoreceptor neurones

Two hundred and eighty-five of the intraoral mechanoreceptor neurones studied were classified as periodontal mechanoreceptor neurones since their properties were typical of those described by previous workers (see Anderson *et al.* 1970). Of these neurones, 260 responded both to forces applied to the teeth in the left side of the

mandible and to electrical stimulation of the left inferior dental nerve and twenty-five responded both to forces applied to the teeth in the left side of the maxilla and to electrical stimulation of the left superior dental nerve. Fig. 2 shows the discharge of a periodontal mechanoreceptor neurone when a supramaximal (1 N) force was applied to the mesial surface of a mandibular left canine tooth.

Fifteen per cent of the periodontal mechanoreceptor neurones studied were rapidly adapting, in that they responded while the force was being applied but did not continue to fire to a sustained force. The other 85% were slowly adapting; they responded to both phasic and sustained components of force. None of the neurones

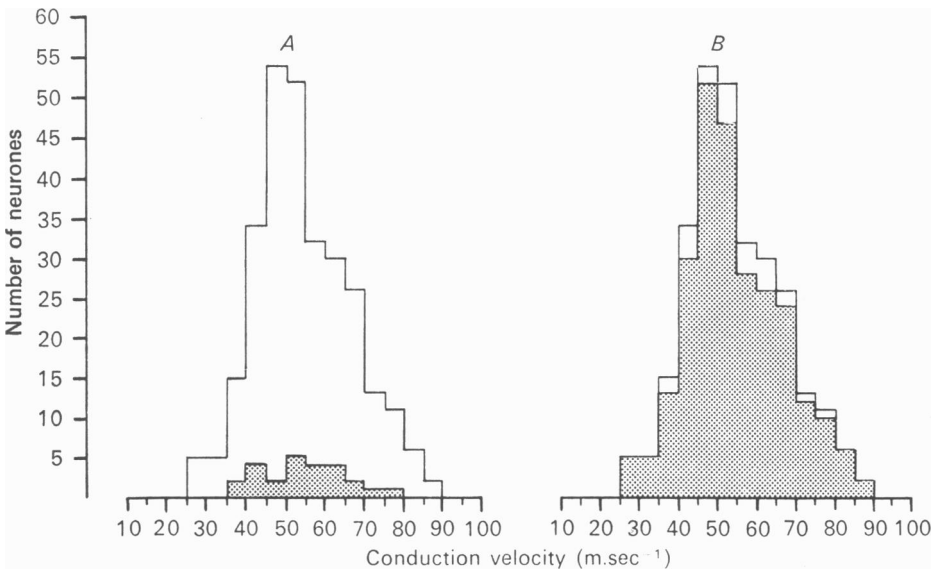

Fig. 3. Distribution of the estimated conduction velocities of the 285 periodontal mechanoreceptor neurones. *A*, maxillary, *B*, mandibular. In both cases the outline of the combined conduction velocities has been superimposed for comparison.

discharged spontaneously. Fifty periodontal neurones tested with the electromechanical transducer ceased to fire between 1 and 10 sec after the application of a sustained supramaximal force (1 N) to the tooth in its most sensitive direction.

All the periodontal mechanoreceptor neurones exhibited directional sensitivity in that they responded maximally to a force on the tooth in one particular direction.

The receptive fields for both maxillary and mandibular periodontal mechanoreceptor neurones were confined to one tooth. No neurone responded to mechanical stimulation of the gingiva only or to both tooth and gingiva. Of the 260 mandibular periodontal mechanoreceptor neurones recorded in the mesencephalic nucleus, 153 responded to forces applied to the canine, fifty-three to forces applied to the molar, and 39, 8, 3, 3 and 1 to forces applied to the second premolar, 1st premolar, 3rd, 2nd and 1st incisors respectively. Fig. 3 shows frequency distribution histograms of the estimated conduction velocities of the 285 periodontal mechanoreceptor neurones studied. The twenty-five maxillary and 260 mandibular neurones are plotted separately for comparison. The range of estimated conduction velocities was from 26 to 87 $m.sec^{-1}$ (mean 54 $m.sec^{-1}$, S.D. 12.1).

'Type P' mechanoreceptor neurones

Forty mesencephalic neurones responded both to electrical stimulation of the left palatine nerve and to forces applied to any of the maxillary teeth, both contralateral and ipsilateral as well as to forces applied to the hard palate and nose. The members

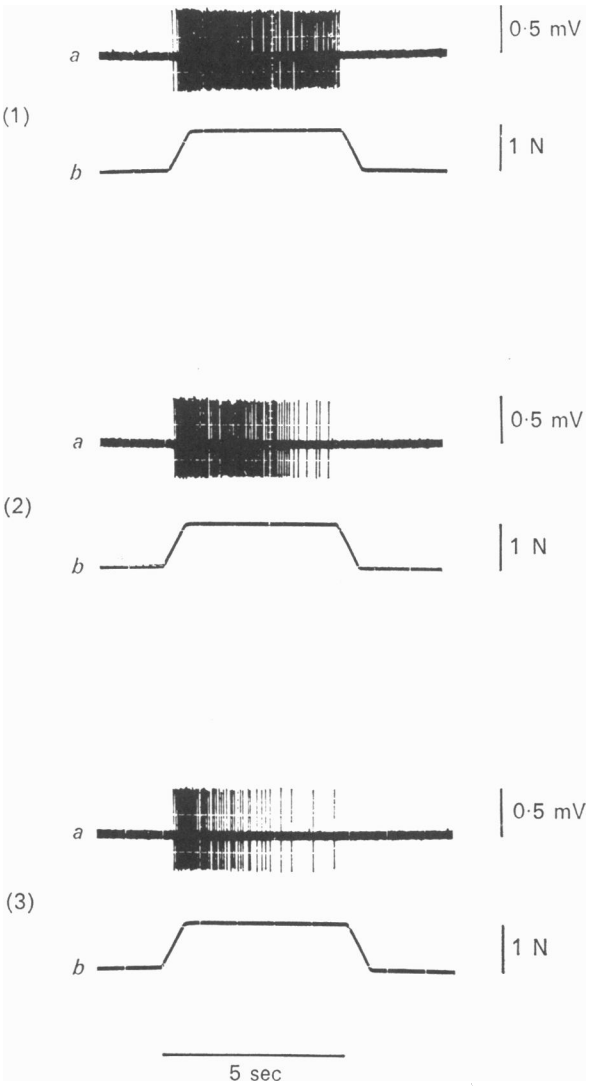

Fig. 4. An example of the responses at a mesencephalic recording electrode (*a*) of a Type P mechanoreceptor neurone to forces (*b*) applied to the (1) ipsilateral maxillary canine, (2) contralateral maxillary canine, and (3) hard palate.

of this group have been termed 'Type P' mechanoreceptor neurones. Fig. 4 shows an example of a record obtained from a typical Type P mechanoreceptor neurone.

All Type P neurones were slowly adapting in that they responded to both phasic and sustained supramaximal forces. No neurones were spontaneously active.

Fig. 5 demonstrates the directional sensitivity exhibited by a Type P neurone. In this example a maximal response could be elicited by applying a force to the labial surface of every tooth in the maxillary arch. There was no response when the force was applied to the palatal surface of the teeth. In general, all neurones from teeth in the maxillary arch responded maximally to forces applied to the teeth in one direction. For example, when the maximal response was obtained by applying a force to the distal surface of the left maxillary canine, the direction of maximal sensitivity for the other teeth in the arch would also be with a force applied to their distal surfaces.

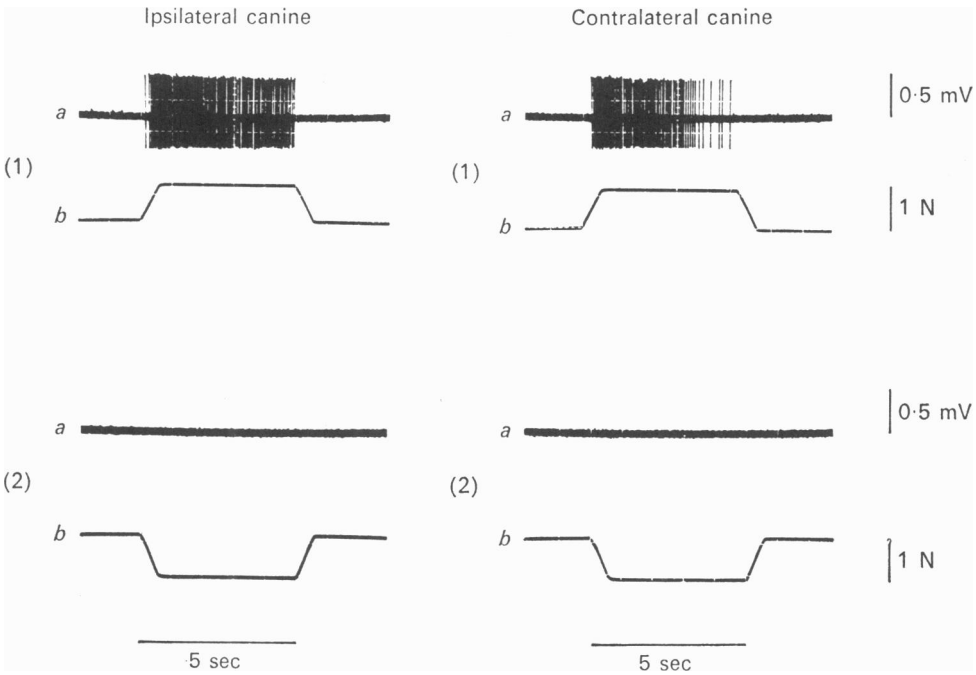

Fig. 5. The response at a mesencephalic recording electrode (*a*) of a Type P mechanoreceptor neurone to forces (*b*) applied to the maxillary canines. (1) The response to a force applied to the labial surfaces of the ipsilateral and contralateral canines. (2) No response to a force applied at 180° to (1), to the palatal surfaces of the teeth.

A characteristic of all Type P neurones was that they produced a greater discharge when a 1 N force was applied to the ipsilateral teeth than when the same force was applied to the contralateral teeth (see Fig. 5). Also all the Type P neurones could be silenced by applying a force to the contralateral canine in the opposite direction to its most sensitive direction whilst a force was being applied to the ipsilateral canine in its most sensitive direction.

A frequency distribution histogram of the conduction velocities of the forty Type P mechanoreceptor neurones with the combined histogram of the conduction velocities of all 325 intraoral mechanoreceptor neurones superimposed for comparisons is shown in Fig. 6. The conduction velocities of the Type P mechanoreceptor fibres were within the range of those for the periodontal mechanoreceptor fibres

(mean, 53·03 m.sec^{-1}; no. 40; S.D. 9·26). The mean conduction velocities of the periodontal mechanoreceptor neurones and the Type P mechanoreceptor neurones were not significantly different ($t = 0{\cdot}81$, $P > 0{\cdot}45$).

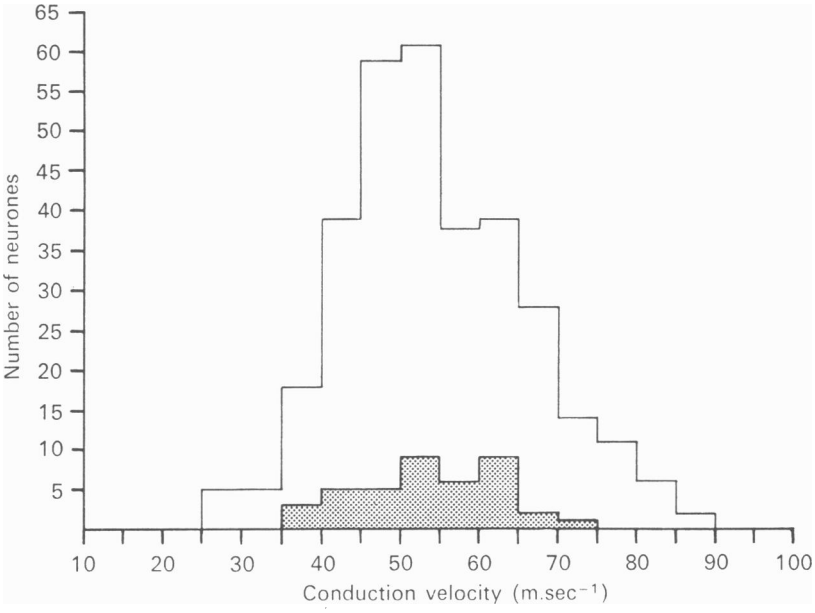

Fig. 6. Distribution of the estimated conduction velocities of the forty Type P mechanoreceptor neurones. The combined histogram of the conduction velocities of all 325 intraoral mechanoreceptor neurones is superimposed for comparison.

Distribution of the neurones within the mesencephalic nucleus

All the neurones, localized by iron marking and determined by their stereotaxic co-ordinates, were situated in the caudal part of the nucleus. Fig. 7 shows the distribution of all 325 intraoral mechanoreceptor neurones recorded from within the mesencephalic nucleus. They have been plotted in the same lateral plane, 2·3 mm from the mid line, as this was where over 80 % of the recordings were made. There is no detectable difference in distribution of the periodontal and Type P mechanoreceptor neurones.

DISCUSSION

The mesencephalic nucleus is considered unique in that it is thought to contain the only known group of primary afferent sensory neurones with their cell bodies located within the central nervous system. The cells which are pseudo-unipolar and have no dendrites, are similar in structure to the neurones of the dorsal root ganglion (Ramon Y Cajal, 1909; Allen, 1919; Clarke, 1926; Schneider, 1928; Weinberg, 1928; Sheinin, 1930).

The degeneration studies of Corbin (1940) and Szentágothai (1948) have shown that many of the sensory fibres in both the maxillary and mandibular division of the trigeminal nerve have their cell bodies in the mesencephalic nucleus and that amongst these are fibres supplying spindles in jaw elevator muscles.

The observation that the properties of the periodontal mechanoreceptor neurones

in the mesencephalic nucleus differ little from those observed in peripheral studies suggests that primary afferent neurones were being studied in these experiments.

During the course of the study, electrophysiological evidence was obtained to provide support to the belief that cell bodies of intraoral mechanoreceptor neurones are present in the mesencephalic nucleus. The following observations were consistent with this view.

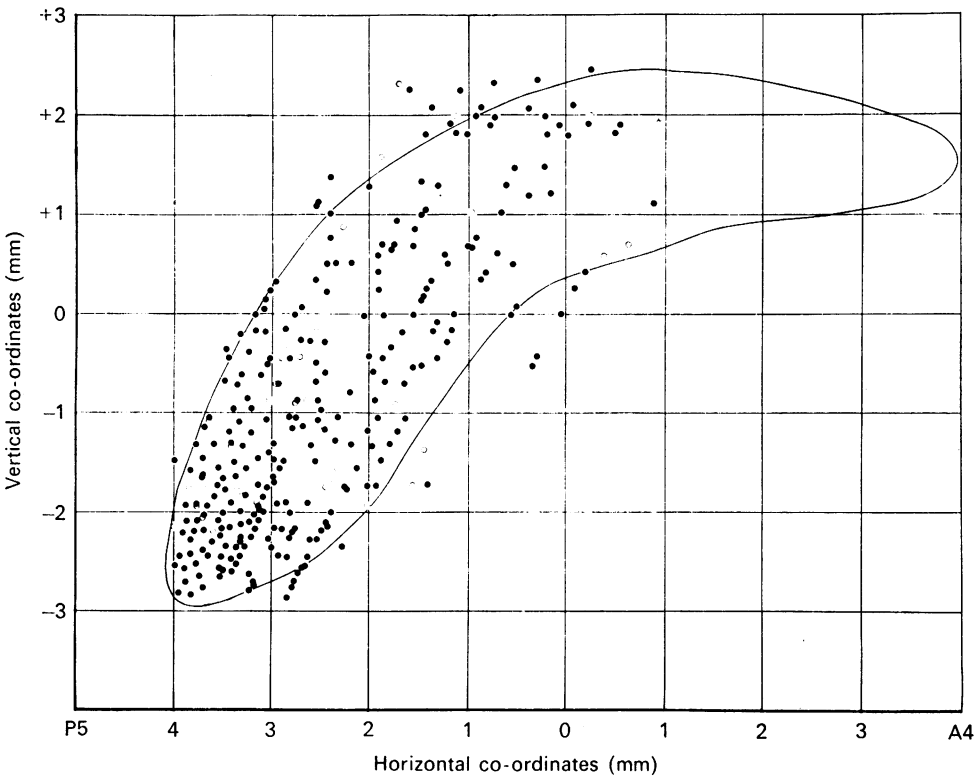

Fig. 7. Map showing the vertical and horizontal co-ordinates of the intraoral mechanoreceptor neurones located in the mesencephalic nucleus at a lateral plane of 2·3 mm from the mid line. The outline is the anatomically defined limits of the nucleus based on Berman (1969). ●, periodontal mechanoreceptor neurones; ○, type P mechanoreceptor neurones.

(*a*) All the recordings were made from the region in which the cells are to be found histologically.

(*b*) All the intraoral mechanoreceptor neurones gave a single all-or-none response to a single electrical stimulus to the peripheral nerve and all were able to follow stimulus frequencies of over 100 Hz for over 2 sec.

(*c*) The latencies of the orthodromic responses evoked by electrical stimulation through the peripheral electrodes, and recorded by the central electrode in the mesencephalic nucleus, were identical to the latencies of the responses propagated antidromically from the central electrode to the peripheral electrodes. Unitary activity was confirmed for both the orthodromic and antidromic conductions by altering the stimulus intensities. All the antidromic responses were able to follow stimulus

frequencies of over 100 Hz for periods of over 2 sec. This evidence is not compatible with the presence of a synapse in the pathway. Furthermore, if a synapse had been traversed one would expect about 0·5 msec to be added to the overall orthodromic conduction delay for a particular fibre. Latencies were recorded as short as 0·7 msec over a conduction distance of 65 mm. If a synapse was present in such a pathway, and assuming a delay of about 0·5 msec for an impulse to traverse a synapse, then the estimated conduction velocity of the fibre would be the unlikely 300 $m.sec^{-1}$.

None of these observations is alone conclusive, but together they provide substantial electrophysiological evidence that primary afferent intraoral mechanoreceptor fibres have their cell bodies in the mesencephalic nucleus. The question arises as to whether the recordings were made from cell bodies or axons. Hubbard, Llinás & Quastel (1969) stated that when an action potential is initiated at a distant point along its axon, and then propagated towards the soma of a neurone which lacks dendrites (as is the case in this study), the electrical change recorded by a micro-electrode near the soma would be triphasic (positive-negative-positive). The action potentials recorded in this study had triphasic waveforms. This does not provide conclusive evidence for the recordings being made from cell bodies but this coupled with the size of the action potentials recorded (0·05–1·5 mV) and the electrode penetration distances over which any one particular response could be recorded (over 100 μm) suggests that the recordings were made from cell bodies and not axons.

Type P mechanoreceptor neurones

Neurones that respond to mechanical stimulation of all the teeth in the maxillary arch and to forces applied to the hard palate and to the nose, have not been reported before in either peripheral or central studies, although Goodwin & Luschei (1975) in a study of jaw elevator muscle spindle afferent units in the mesencephalic nucleus noted, in passing, that some maxillary mechanoreceptor neurones had receptive fields which extended over the whole maxillary arch. All the Type P mechanoreceptor neurones identified in this study responded to electrical stimulation of only one nerve trunk, the palatine. Corbin (1940) has shown that there was degeneration of nerve fibres in the palatine nerve after placing lesions in the mesencephalic nucleus and tract, suggesting that there were in the nucleus some cell bodies of primary afferent neurones that had fibres running in the palatine nerve. This study has confirmed that observation electrophysiologically.

The greatest difference between the Type P and periodontal mechanoreceptor neurones lies in their receptive fields. The possibility that the palatine nerve branches to serve receptors around all the teeth on both sides of the maxillary arch seems unlikely according to available anatomical data. A more likely explanation would be that the receptors are situated in sutural tissue and that a force applied to any maxillary or supra-maxillary structure is transmitted through the bone to the receptors. From the data obtained in this study one can only speculate as to the site of the receptors. One possible site is the palatomaxillary suture, as the forces exerted on a canine tooth are distributed across the fibrous palatomaxillary suture and not along the mid line sutures (Buckland-Wright, 1977). It is not possible at present to predict whether the receptors respond to either compression or tension of

the surrounding tissues. However, the hypothesis that these Type P mechanoreceptors are situated in sutural tissue seems to be the most likely.

Periodontal mechanoreceptor neurones

Jerge (1963) reported the absence in the mesencephalic nucleus of very slowly adapting mechanoreceptor neurones similar to those found in the peripheral studies by Pfaffmann (1939), Ness (1954) and later confirmed by Hannam (1968*a*, 1969).

During the course of the study it was possible to test fifty canine periodontal mechanoreceptor neurones with a controlled mechanical stimulation. Using rather more precise methods than those adopted by Jerge, it was possible to conclude that no cat's canine periodontal mechanoreceptor neurone that fired for longer than 10 sec to a prolonged 1 N force to the tooth was located in the mesencephalic nucleus. Jerge reported that the average force required for activation of a neurone was 1·8 g (17·6 mN) with values ranging between 1 g (9·8 mN) and 3 g (24·9 mN). Studies by Kerr & Lysak (1964) and Beaudreau & Jerge (1968) have demonstrated the presence of more slowly adapting periodontal mechanoreceptor neurones in the Gasserian ganglion.

No spontaneously active intraoral mechanoreceptor neurones have been reported in this or other studies on the mesencephalic nucleus nor have they been reported in studies on the Gasserian ganglion. On the other hand spontaneous activity has been found in most of the peripheral studies (see Anderson *et al.*, 1970). This raises the question as to the possible explanation for the differences between data from peripheral nerve, and data from studies on the Gasserian ganglion or mesencephalic nucleus. Much of the work on spontaneously discharging mechanoreceptor neurones has been obtained from peripheral nerves of dogs, whereas most of the central recordings have been performed on cats. There might be a species difference, although some spontaneous activity has been reported in peripheral studies in the cat (Sakada & Onodera, 1974). A second, but unlikely possibility is that there is a third collection of intraoral mechanoreceptor cell bodies situated somewhere else which includes those of spontaneously discharging neurones. A third, and at present the most likely, possibility is that spontaneous activity is an experimental artifact, due to some technical or physiological difference in the experimental conditions between central and peripheral studies. One possible difference is that in recordings made from the mesencephalic nucleus or the Gasserian ganglion, efferent pathways which have been shown to influence intraoral mechanoreceptor activity (Anderson & Linden, 1977) remain intact, whereas in the more peripheral recordings the relevant autonomic axons are cut along with the peripheral nerve bundle.

The receptive fields for the periodontal mechanoreceptor neurones identified in this study were similar to those described in peripheral studies, in that they were confined to one tooth. Jerge (1963) found that nineteen out of his sample of twenty-four mechanoreceptor neurones responded to forces applied to the canines. Corbin & Harrison (1940) noted, when they recorded from this nucleus, that pressure to the canines produced a bigger response than did pressure to any other oral structure; they were recording the gross response and not single unit activity. In the present series of experiments the canine had the largest representation in the mesencephalic (over 50 % of those represented in the inferior dental nerve). Kruger & Michel (1962) and

Kawamura & Nishiyama (1966) observed that the majority of cells in the main sensory and spinal nuclei also responded to forces applied to the canines. The functional significance of this observation is not immediately apparent.

The range of conduction velocities of the periodontal mechanoreceptor neurones, between 26 and 87 $m.sec^{-1}$ with a mean of 55 $m.sec^{-1}$, agrees well with previous estimates in peripheral nerve studies (Pfaffmann, 1939; Hannam, 1968*b*).

Distribution of the neurones within the nucleus

All 325 intraoral mechanoreceptor neurones were found in the caudal part of the nucleus. This observation is in complete agreement with those of Corbin (1940) and Cody, Harrison, Taylor & Weghofer (1974). On the other hand, Jerge (1963) found some periodontal mechanoreceptor neurones in the rostral part of the nucleus. The significance of the distribution of the intraoral mechanoreceptors within the nucleus can only be speculated. Cody *et al.* (1974) suggested that it may have some significance in relation to possible electrotonic coupling between cells of the caudal part of the nucleus. There is, however, no evidence from the electrotonic studies (Hinrichsen, 1970; Baker & Llinás, 1971) for the coupling being predominantly in the caudal part of the nucleus.

Both Hinrichsen, and Baker & Llinás reported that fibres in the masseteric branch of the trigeminal nerve were involved but did not show whether the coupling was between two muscle spindle cells or muscle spindle and intraoral mechanoreceptor cells. If there was electrotonic coupling between muscle spindle and intraoral mechanoreceptor cells one would expect to record from single neurones that respond to both opening of the mouth and mechanical stimulation of the teeth. During the course of this study every neurone was tested to see if it responded to both jaw opening and mechanical stimulation of the teeth. None of the 325 intraoral mechanoreceptor neurones was found to respond to both forms of stimuli. This suggests that if coupling does exist between cells in the mesencephalic nucleus of the cat that it is not between intraoral mechanoreceptor and muscle spindle cells.

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