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BRANCHING OF MUSCLE SPINDLE AFFERENTS OF JAW CLOSING MUSCLES IN THE CAT

BY T. KATO, Y. KAWAMURA AND T. MORIMOTO*

From the Department of Oral Physiology, Dental School, Osaka University, 3–48, Nakanoshima 4-Chome, Kitaku, Osaka, 530 Japan

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SUMMARY

1. Functionally isolated single fibres were prepared from the cut central ends of the masseter nerve in cats. Of those firing in response to muscle stretch, most were alpha motor units but some had the properties of afferent fibres innervating muscle receptors.

2. These afferent units were remarkably sensitive to muscle stretch even under anaesthesia deep enough to eliminate all stretch evoked e.m.g. activity in masseter. Moreover, these units responded to gentle pressing of the surface of either the masseter, temporalis or pterygoid muscles.

3. On the basis of their responses to ramp stretch, to high-frequency vibration, to suxamethonium, and to gentle pressing of the muscle surface, the majority were considered to arise from primary or secondary endings of muscle spindles.

4. In reflexly induced jaw movements, the highest discharge frequency of these spindles was observed during the jaw opening phase. However, they were also activated during the jaw closing phase, indicating that the fusimotor innervation to the source spindle was still preserved.

5. From these results, it is concluded that branching of the spindle afferent outside the capsule occurs in the muscle nerve innervating cat's jaw closing muscles.

INTRODUCTION

The masseter nerve of the cat is frequently used for studies on neurophysiological mechanisms of masticatory movements. For analysing activities of jaw closer motoneurones, functionally isolated single fibres are often prepared from the cut central ends of the masseter nerve (Abe, Takata & Kawamura, 1973; Appenteng, Morimoto & Taylor, 1980). In such preparations, units are occasionally found which respond to muscle stretch with far more sensitivity than the ordinary alpha motor units, and behave like muscle spindle afferents. If they do indeed originate from muscle spindles, it is possible that the recorded discharges are impulses conducted antidromically in branches of the parent axon to the spindle. Most sensory axons subserving various sensory modalities have branchings close to their receptors (Lindblom, 1958; Millar, 1971; Duclaux & Kenshalo, 1973; Floyd & Morrison, 1974; Horch, Whitehorn & Burgess, 1974; Matthews, 1977; Fukami, 1980). However, the

* Authors' names are in alphabetical order.

afferents to the sensory endings in the mammalian muscle spindles, especially Ia fibres to the primary ending, rarely branch prior to entering the capsule of individual spindles (for review, Matthews, 1972; Barker, 1974). On the other hand, branching of the primary spindle afferents has been found in the rat's masticatory muscles both outside and inside the capsule (Karlsen, 1965).

In the present study, an attempt has been made to substantiate such branching of spindle afferents outside the capsule by analysing physiological properties of the highly stretch-sensitive units found in the cut central ends of branches of the masseter nerve.

METHODS

Preparation of animals

Twenty-three cats (1·7–3·2 kg) were initially anaesthetized with sodium pentobarbitone (Somnopentyl, Pitman-Moore, 30 mg/kg, I.P.) and supplementary doses of thiamylone sodium (Isozol, Yoshitomi Pharm. Co., 15 mg/ml, I.V.) were given when necessary. Tracheal and venous catheters were inserted and rectal temperature was maintained at 37–38 °C by the heating pad. Pairs of enamelled copper wires, with their terminal 5 mm bared, were inserted into the temporalis and masseter muscles for e.m.g. recording. The head was supported right side down by means of a metal plate screwed to the skull, so as to cause less noxious stimulation than the usual head clamp. The left masseter nerve was exposed by partly detaching the masseter muscle from its insertion into the zygomatic arch. Under the dissecting microscope, the masseter nerve was then carefully separated from the surrounding muscles. This nerve usually has four or five anterior branches, three superficial branches and three or four posterior branches. The anterior and superficial branches were mainly used in the present study.

Recording

Discharges of functionally isolated single fibres were recorded from the cut central end of intramuscular nerve filaments immersed in liquid paraffin. The recording electrode was a bipolar platinum electrode of 1 mm interpolar distance. The 'centre triggered averaging' method, which is fundamentally similar to the 'back averaging' technique (Kirkwood & Sears, 1975*a*, *b*; Appenteng *et al.* 1980), was employed for identification of the course of the recorded filament or for conduction velocity measurements of some units. For this purpose, another bipolar platinum electrode of 1·5 mm interpolar distance was placed proximally on the main nerve trunk of the masseter nerve. A unitary discharge recorded by the distal electrode was used as a triggering pulse to trigger an averager receiving the neurogram recorded by the proximal electrode. The triggering point was located at the centre of the averaged neurogram using a computer with signal delay (ATAC 2300, Nihon-kohden Co.) so that the events occurring before and after the triggering pulse could be observed. The conduction distance was measured on each unit between the proximal pole of the two electrodes, which ranged from 9 to 14 mm in the present study. The conduction time was taken as the interval between the onset of the triggering spike and that of the centre triggered averaging-response at the nerve trunk.

Jaw movements in the vertical direction during reflex swallowing were recorded by a position transducer consisting of a light-emitting diode (GL-410, Sharp Co.) mounted on the right mandibular body and a phototransistor (PT-410F, Sharp Co.) on the right zygomatic arch.

Application of mechanical stimuli to the masticatory muscles

Mechanical stimuli such as ramp stretch and vibration were applied to jaw closing muscles by an electromagnetic servo stretcher (EMIC 513A, Shin-nihon Sokki Co.). This stretcher was connected to the mandible using a steel pin inserted at the left premolar region, 40 mm from the condylar axis of the temporomandibular joint. The amplitudes of muscle stretch and of vibration were regulated with a d.c. amplifier (EMIC 381A, Shin-nihon Sokki Co.), and the frequencies of vibration were controlled with a function generator (458A, Kikusui Elect. Co.).

Muscle contraction

Pairs of enamelled wires used for recording e.m.g. activities of the temporalis and masseter muscles were also used for causing twitch contraction of these muscles. A square pulse of 2 ms was delivered repeatedly at 0·5 Hz. The force of contraction was recorded by a force-displacement transducer (FD-1P, Nihon-kohden Co.) connected to the mentum.

Suxamethonium (SCh) administration

SCh (200 μg/kg) was intravenously administered through the cannula inserted into the left superficial radial vein. Animals were artificially ventilated. Pancuronium bromide (Mioblock; Organon, 20 μg/kg) was given previously in order to eliminate disturbances from jerky movements of the animal.

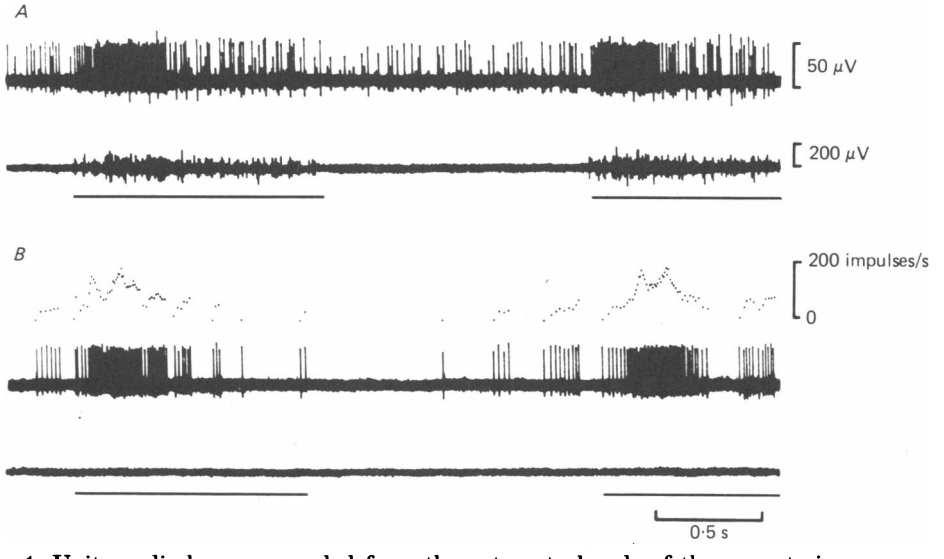

Fig. 1. Unitary discharges recorded from the cut central ends of the masseteric nerve branch in response to passive muscle stretch, before (*A*) and after (*B*) deepening anaesthesia. The jaw-closing muscles were stretched by manual jaw depression during the period indicated by the underlying bars. Note the unit still responded well to the muscle stretch with anaesthesia deep enough to prevent stretch reflex e.m.g. activity in the masseter muscle.

RESULTS

When recordings were made from the cut central ends of the masseter nerve branch, many units were found to respond to passive jaw opening, which stretched the jaw closing muscles (Fig. 1 A). The majority of these stretch-sensitive units were believed to be alpha motor units because their response was abolished by deepening anaesthesia. As shown in Fig. 1 *B*, however, some units still responded well to the muscle stretch with anaesthesia deep enough to prevent stretch reflex e.m.g. activity in the masseter. Some of these anaesthesia-resistant units increased their firing to more than 200 Hz during muscle stretch, which was much greater than the range of firing frequency observed in alpha motoneurones. They also had a very low threshold to stretch as shown by their response to the very slight jaw movements occurring during spontaneous respiration. On the other hand, they showed a pause in discharge during muscle twitches.

A total of twenty-six units of this type were obtained in this study. Although functionally isolated single units were not always recorded, multiple unit recordings exhibited the presence of this type of unit in every cat.

Pressure-sensitive spot on the muscle surface

Like muscle spindle afferents recorded in the trigeminal mesencephalic and motor nuclei (Goodwin & Luschei, 1975; Sessle, 1977; Appenteng *et al.* 1980), the above units responded to gentle probing of the muscle surface with a small tipped (diameter *ca.* 1 mm) glass rod (Fig. 2*B* and *D*). Although records were made from the masseter

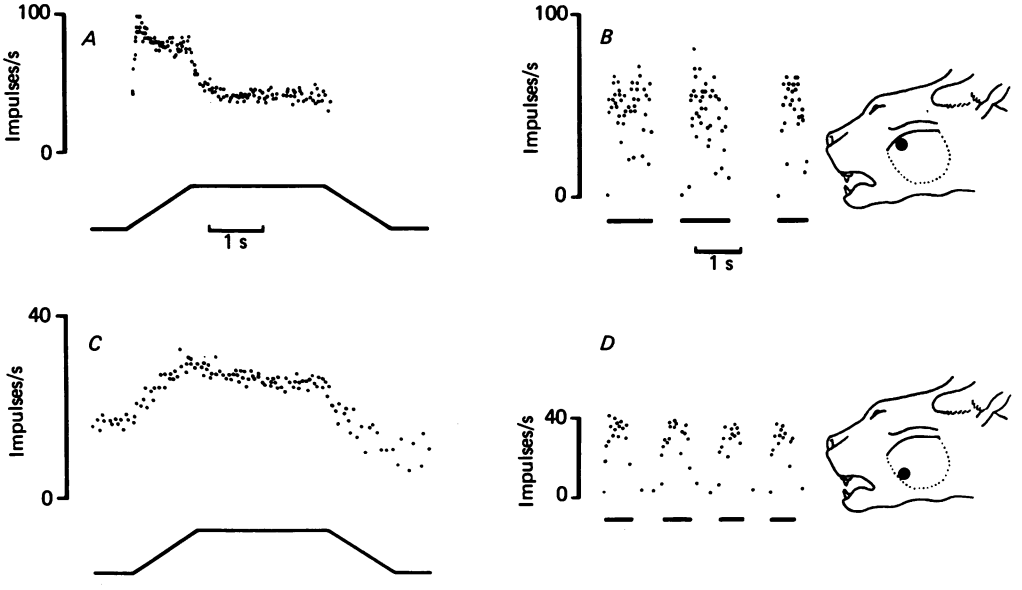

Fig. 2. Two typical examples of the response to jaw opening (*A*, *C*) and to probing of the muscle surface (*B*, *D*). *A*, the response of a putative spindle primary afferent to 6° of jaw opening at a rate of 4·5 deg/s. The unit showed no spontaneous discharges but a marked dynamic response appeared during the stretching phase. On releasing the stretch, the firing ceased immediately. *B*, the response of the same unit as *A* to probing of the muscle surface below the zygomatic arch. *C*, the response of a putative spindle secondary afferent to jaw opening. A small dynamic response appeared during the stretching phase. On releasing the stretch, the unit gradually decreased in firing rate. *D*, the response of the same unit as *B* to probing of the anterior belly of the masseter muscle.

nerve, pressure-sensitive spots were not solely confined to the masseter muscle. Of the total twenty-six units, thirteen were identified as lying in the masseter and seven in the temporalis muscles. Five units responded exclusively to pressure on the upper eyelid and the remaining one to pressure on the soft palate. The former may arise from receptors in the anterior part of the temporalis muscle and the latter from receptors in the pterygoid muscles. From the following finding, however, it seems unlikely that probing of the temporalis muscle causing mechanical deformation of the masseter muscles resulted in excitation of masseteric sensory receptors. In the unit whose pressure sensitive spot was in the temporalis, the response to a ramp stretch and to probing of the muscle surface was still elicited after dissection of all the branches of the masseter nerve from its trunk except for the recorded one.

Units were designated as masseter, temporalis or pterygoid units, according to the location of the spot most sensitive to pressure.

Response to a muscle stretch after dissection of the masseter nerve trunk

The above findings suggest that the highly stretch-sensitive units were neither alpha nor fusimotor units but rather afferent units from muscle spindles. The following results further proved that these units were indeed muscle afferents. Fig. 3*A* shows

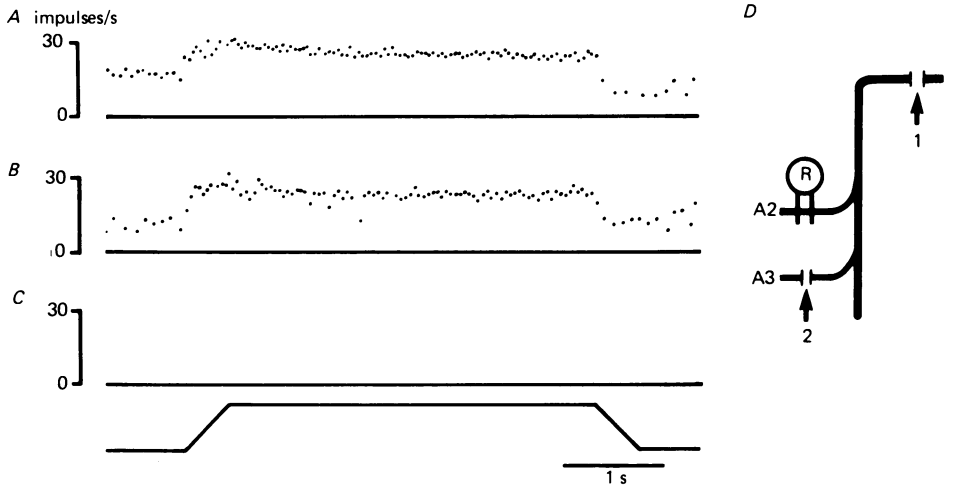

Fig. 3. The effect of nerve dissection of the response of the putative spindle afferent to jaw opening. *A*, control response. *B*, remaining response after dissection of the main trunk close to the mandibular notch (Arrow 1 in *D*). *C*, disappearance of the response after dissection of the neighbouring branch (Arrow 2). *D*, schematic illustration of the masseter nerve branching. The recording electrode is shown by R.

the response of the unit to a ramp stretch which was recorded from the second anterior branch (A2). This response was still observed even after division of the main trunk close to the mandibular notch (Fig. 3*B*). Since the central connexion of the recorded filament was lost by this procedure, the above result apparently indicates that the unit was not recorded from an efferent but from an afferent. However, the response to muscle stretch disappeared after severance of the third anterior branch (A3) which is the next branch distal to the recorded one (Fig. 3*C*). Therefore, impulses recorded from A2 originated from a spindle ending innervated by A3. Similar experiments with division of the masseter nerve trunk were performed on five masseter units and three temporalis units. Responses of the masseter units were preserved after dissection whereas those of the temporalis units disappeared. These results indicate that discharges of the masseter unit arose from sensory endings in the masseter muscle.

Classification of afferent units

Attempts were made to identify the sensory modalities of the afferent units by the responses to: (*a*) ramp stretches; (*b*) vibration; (*c*) suxamethonium (SCh) administration (200 μg/kg). Two typical examples of the response to 6° of jaw opening at a rate of 4·5 deg/s are shown in Fig. 2: one showed a prominent dynamic response during the stretching phase (Fig. 2*A*), and the other showed a small dynamic response

(Fig. 2*C*). These two types of responses were comparable to those described previously for spindle endings; the former most resembling typical primary and the latter secondary endings behaviour. The velocity sensitivity was assessed by measuring the dynamic indices (Crowe & Matthews, 1964) to stretch rates of 2, 4·5, 6·8, 9·1, 11·1, 14·5 and 21·5 deg/s. All stretches were 6·1° starting from the initial 15° of opening. Assuming the relationship between the dynamic index and the rate of stretch to be linear, the slope of the regression line for each unit gives the velocity sensitivity. The distribution of sensitivities of fifteen units ranged from 0·2 to 7·53 impulses/s per deg/s of movement.

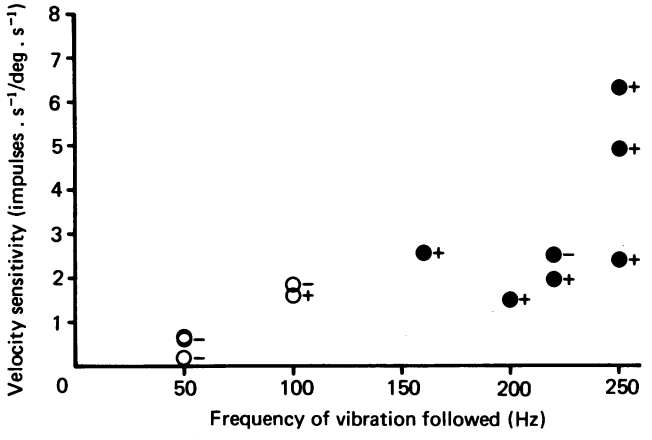

Fig. 4. The effect of SCh and the relationship between the velocity sensitivity and the maximum frequency of vibration followed. Filled circles are the units which gave one impulse per cycle of vibration. Open circles are the units which did not respond to the frequency of vibration tested. The plus and minus signs indicate facilitatory and nil effects of SCh, respectively. Note that most of the units which followed vibration at a frequency higher than 160 Hz tended to have a greater velocity sensitivity and were more susceptible to SCh than the units which were unable to follow vibration of the frequency below 100 Hz.

The maximum frequency of vibration followed was examined by increasing frequencies up to 250 Hz in 10 Hz increments. The amplitude of stretch was 200 μm at frequencies below 100 Hz, 100 μm between 110 and 200 Hz, and 50 μm above 210 Hz. Out of twenty units examined, eleven followed higher than 160 Hz and one followed 100 Hz, but the remaining eight failed to respond to frequencies below 100 Hz.

The effect of SCh on the resting discharge and on the dynamic index of the putative spindle afferents were tested in eighteen units. Ten units were facilitated both in the resting discharges and the dynamic index, and seven were not affected by SCh. In the remaining one unit, the resting discharge was facilitated while the dynamic index was reduced 1 min after SCh administration. In Fig. 4, the effect of SCh and the relationship between the maximum frequency of vibration followed and the velocity sensitivity are shown for twelve units including one unit on which the effect of SCh was not tested. Filled circles indicate the units which could give one impulse per cycle of vibration tested while open circles are the units which did not respond to the frequency of vibration tested. The plus and minus signs indicate facilitatory and nil

effects of SCh, respectively. This graph shows that most of the units which followed vibration at a frequency higher than 160 Hz tended to have a greater velocity sensitivity and were more susceptible to SCh than the units which were unable to follow vibration of the frequency below 100 Hz. Based on these findings, it may be concluded that the former are spindle primary afferents and the latter are spindle secondary afferents. Therefore, both spindle primaries and secondaries were included in the recorded units.

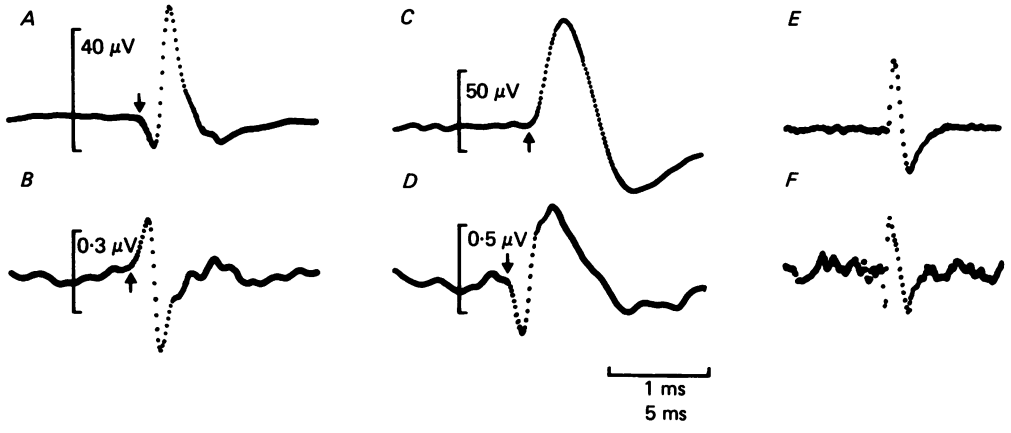

Fig. 5. Preservation of central connexion of spindle afferents proved by the 'centre triggered averaging' method. The averaged responses of the triggering spike (*A*, *C*, *E*) and those of the nerve trunk (*B*, *D*, *F*). *A* and *B* were the responses of a masseter unit, and *C*, *D*, *E* and *F* were those of a temporalis unit. Appearance of the nerve trunk response indicates the branching of the spindle afferent to occur in the masseter nerve. Note that the triggering spike and the nerve trunk response appeared almost simultaneously in the masseter unit, while the latter slightly preceded the former in the temporalis unit. Time scale: 1 ms for *A*, *B*, *C* and *D* and 5 ms for *E* and *F*.

Identification of the ascending pathway

There are two possible pathways for transmitting impulses from these endings to the recorded fibre. One is the branching of the parent axon and the other is the straying of the afferent or the communicating fibre to form a loop into another branch. If the former is the case, the parent axon preserves its central connexion even after section and preparation of the recorded fibre while in the latter case, the afferent would lose its central connexion. In order to examine the presence or the absence of the central connexion of the isolated filament, the 'centre triggered averaging' method was employed (see Methods). If the unit preserves the central connexion, an averaged response will appear at the nerve trunk. Examples of the averaged response of the triggered spike and that of the nerve trunk of the masseter unit are illustrated in Fig. 5*A* and *B*, respectively. As shown here, the response appeared at the nerve trunk, indicating the branching of the muscle spindle afferent to occur in the masseter nerve of the cat. Moreover, the time interval between the triggering spike and the nerve trunk response of seven masseter units ranged from 0 to 0·3 ms. Such short time intervals imply that the impulses from the source spindle arrived almost

simultaneously at the two electrodes. This finding is also compatible with the idea of branching of the spindle afferent. The averaged response of the triggering spike and that of the nerve trunk of a temporalis unit are shown in Fig. 5*C* and *D* respectively, and also in Fig. 5*E* and *F* with longer time bins. In the temporalis units, the nerve trunk response always appeared earlier than the triggering spike, indicating that impulses descended through the nerve trunk to the recorded filament. By

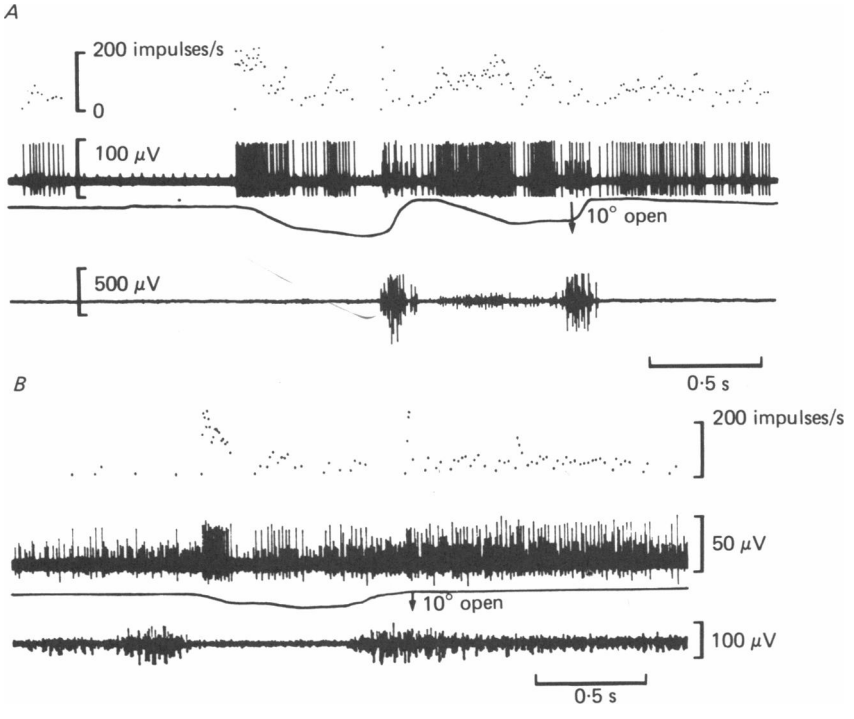

Fig. 6. Behaviour of two spindle afferents (*A*, *B*) during reflex jaw movements. The firing frequency of the largest unit (the masseter unit) in both *A* and *B* is shown by the dots above each neurogram. The e.m.g. activity in *A* and *B* was recorded from the masseter and temporalis muscles, respectively. The masseter units fired not only during the passive stretching phase of the muscle but also during the active contraction phase, this finding indicating preservation of fusimotor innervation to the source spindle.

measurement of the conduction distance between two electrodes, conduction velocities were assessed on seven temporalis units, and ranged between 28·5 and 55 m/s. These values are comparable to the range already reported on muscle spindle afferents of jaw closing muscles (Appenteng *et al.* 1980; Inoue, Morimoto & Kawamura, 1981).

Behaviour of the spindle afferent during reflex jaw movements.

Since the parent axon to the source spindle is kept intact even after preparation of the nerve fibre, the fusimotor innervation to the spindle also may be preserved. In order to confirm this assumption, the behaviour of these afferent units was studied during reflex swallowing in which trigeminal fusimotor fibres are activated (Appenteng *et al.* 1980). For this purpose, animals were maintained at a light level of anaesthesia

according to the method of Appenteng *et al.* (1980). Placing 1 ml of dilute alcohol in the mouth produced single or repetitive jaw movements as shown in Fig. 6. The largest unit in Fig. 6*A*, the masseter unit, fired at a rate higher than 200 Hz at the beginning of the jaw opening when there was no masseteric e.m.g. activity. During subsequent jaw closure, this unit also fired although the discharge frequency was far less than during the jaw opening phase. In this animal, two successive jaw openings were produced by placing fluid in the mouth. The firing frequency during the second

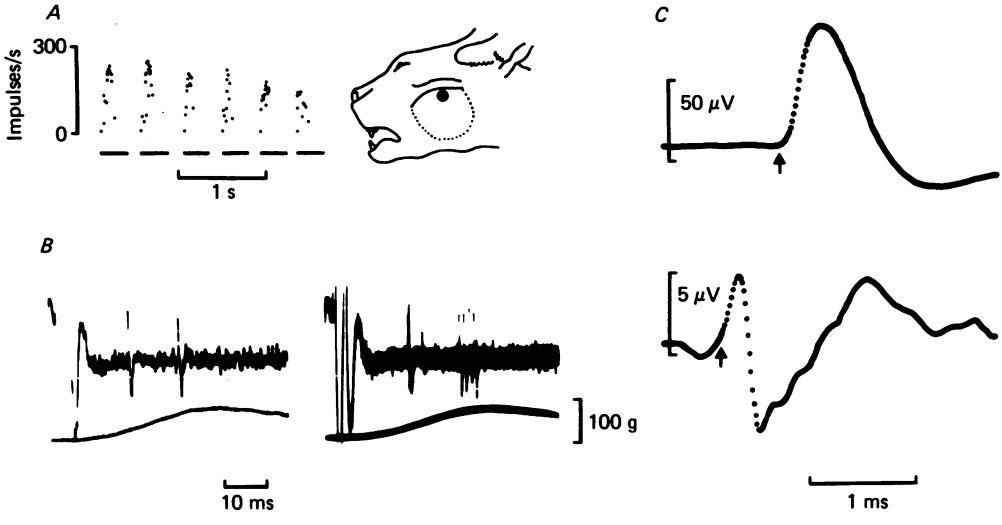

Fig. 7. Physiological properties of a putative tendon organ afferent. *A*, the response to probing the masseter muscle surface below the zygomatic arch. The unit adapted very rapidly. *B*, the response to twitch contraction of the masseter muscle. Two spikes appeared on the rising phase of muscle contraction. On the right is shown the superimposed record of five sweeps. *C*, the averaging responses of the triggering spike (upper trace) and of the nerve trunk (lower trace). The appearance of the nerve trunk response indicates preservation of the central connexion of the recorded filament, and thus the branching of the parent axon to this type of receptor also occurs.

opening was higher than that during the first jaw opening in spite of the fact that the degree of opening was greater in the latter than in the former. It should be noted that the second jaw opening was accompanied by some e.m.g. activity in masseter while no e.m.g. appeared during the first cycle of jaw movements. Another example of the behaviour of a masseter unit during reflex swallowing is shown in Fig. 6*B*. The firing pattern of the largest unit was fundamentally similar to that of the unit shown in Fig. 6*A*. It is pointed out that, during sustained jaw closure after swallowing, the unit maintained its firing at about 50 Hz in the presence of some temporalis e.m.g. activity. The above two examples showed that the spindle afferents were activated not only during the passive stretching phase of the muscle but also during the active contraction phase. Therefore, fusimotor innervation to the source spindle was found to be preserved even after preparation of the nerve fibre.

Response of afferents from other muscle receptors

In addition to the above mentioned spindle afferents, we observed on two occasions units which responded to probing of the surface of the masseter muscle (Fig. 7*A*) and to muscle contraction (Fig. 7*B*) although the response to the former adapted rapidly. On the other hand, this unit did not readily respond to a muscle stretch nor to vibratory stimuli in the stimulus range tested. Moreover, SCh had no effect on this type of unit. These physiological properties were apparently different from those of muscle spindle endings and Pacinian corpuscles but may be those of 'high-threshold' Golgi tendon organs (Dutia & Ferrell, 1980). As shown in Fig. 7*C*, the centre triggered averaging method revealed that the central connexion to this afferent was preserved after preparation of the recorded filament, indicating that branching of the parent axon to this type of receptor also occurs.

DISCUSSION

The present study revealed that the stretch-sensitive units found in the cut central ends of the masseter nerve were not always alpha motor units but occasionally afferent units from muscle receptors. In contrast to the alpha motor units, these afferent units were very resistant to general anaesthesia and, in some cases, discharged at a rate higher than 200 Hz during a muscle stretch, which is beyond the range of frequency modulation of alpha motor units. Moreover, they fired more vigorously in the jaw opening phase than in the jaw closing phase during reflex swallowing. On the basis of their responses to muscle stretches, their following of high-frequency vibration, susceptibility to SCh and also the response to gentle probing of the muscle surface, the majority of them were identified as arising from primary or secondary endings of muscle spindles. The most plausible anatomical explanation of recording discharges of spindle afferents from the cut central ends of the masseter nerve is the branching of these afferents. The straying of an afferent or the communicating fibres to other nerve branches is improbable because the central connexion of these afferents was still preserved after preparation of the nerve fibre (Fig. 3).

Terminal ramification of the sensory axon is commonly observed among various sensory modalities (Tower, 1940; Lindblom, 1958; Millar, 1971; Duclaux & Kenshalo, 1973; Floyd & Morrison, 1974; Horch *et al.* 1974; Matthews, 1977). The spindle afferent also shows ramification inside the capsule, supplying sensory endings on the intrafusal fibres. Outside the capsule, however, branching of the spindle afferents is uncommon. Barker (1962) found branching of an afferent supplying primary endings to two spindles lying near together but such instances were reported to be extremely rare. Eccles & Sherrington (1930) demonstrated increase in the number of the afferents of the muscle nerve, as followed distally in the nerve trunk before it reaches the muscles, suggesting that branching of the afferent might occur. However, when a Ia fibre was traced from a spindle in the piriformis muscle to the dorsal root ganglion, no branching was found to occur (von Thiel, 1959). Tracing back from the spindle to the intramuscular nerve trunk of mouse muscles, Wohlfart & Henriksson (1960) found no ramifications in the spindle primary afferent, while the secondary

spindle afferent was often found to be branched and sometimes innervated more than one spindle. On branching of the secondary spindle afferents, however, Barker, Ip & Adal (1962) reported that only eight out of 279 secondary spindle afferents in the cat's soleus muscle branched when traced 0·5–4·0 mm from their spindles. Stacey (1969) found no intramuscular branching to occur in forty secondary fibres in the cat's hind limb muscles. Moreover, the fibre-to-ending ratios for primary endings and group Ia fibres and for secondary endings and group II fibres are usually one to one (Barker, 1962, 1974). In contrast to these findings, Karlsen (1965) histologically observed branchings occurring extensively in the rat's jaw muscles although mostly inside the capsule. In some human muscles, similar observations were made by Cooper & Daniel (1963). The present study revealed physiologically that branching of the primary as well as the secondary spindle afferents is not uncommon in the masseter nerve of the cat.

The branching point of spindle afferents is not reported by Karlsen (1965). In the units recorded here, however, the branching point was not always so close to individual muscle spindles because the nerve fibre used for recording and the one innervating the source spindle were found in different branches (Fig. 3). On the other hand, the branching point was not always within the brain stem because the masseter units still responded to a muscle stretch after section of the nerve trunk just before it crossed the mandibular notch. The branches of a single parent axon of the sensory nerve generally innervate receptors of the same modality. Therefore, the nerve fibre from which the spindle units were recorded in the present study would probably have terminated on another spindle ending: a single spindle afferent may thus innervate at least one pair of muscle spindles. If this is the case, interaction among impulses conducting along each branch may occur at the branching point. The mesencephalic trigeminal neurones which receive spindle inputs from jaw-closing muscles are not always clearly separable into groups corresponding to primary and secondary spindle units either by conduction velocity measurement or by functional criteria other than activation by SCh or vibration (Cody, Lee & Taylor, 1972; Inoue *et al.* 1981). It is possible that in some cases interactions between impulses from a pair of spindle endings prevent a clear separation of these endings into two categories.

Some spindle afferents in the masseter nerve were found to respond to gentle probing of the temporalis muscles. Mechanical deformation of the masseter muscle due to this procedure could be excluded in the present study. There are two possible explanations for the above finding: one is the branching of the temporalis spindle afferent to the masseter nerve and the other is the electrotonic coupling between ganglion cells of spindle afferents originating from two different muscles. The presence of electrotonic coupling has been verified physiologically and histologically in the mesencephalic trigeminal nucleus (Hinrichsen, 1970, 1976; Barker & Llinás, 1971), although modalities of sensation to which the coupling cells are related are still unknown. It cannot be decided from the present findings whether electrotonic coupling could be strong enough to cause a one-to-one firing of one cell by another, but it seems unlikely.

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