J. Physiol. (1980), **305**, *pp.* 415–431
With 8 *text-figures*
Printed in Great Britain

FUSIMOTOR ACTIVITY IN MASSETER NERVE OF THE CAT DURING REFLEX JAW MOVEMENTS

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(*Received 21 November 1979*)

SUMMARY

1. Unit recordings have been made from the central ends of filaments of the masseter nerve in lightly anaesthetized cats. Evidence is presented to show that fusimotor activity may be distinguished from α motor activity.

2. During reflex cyclic movements induced by intra-oral stimulation, two distinct patterns of fusimotor firing emerged. One type of unit increased firing at the beginning and sustained this with little modulation throughout the movements. The other type was strongly modulated approximately in parallel with the α motor activity.

3. By comparison with records of jaw elevator spindle afferents under similar conditions, it was deduced that the sustained type of action was due to dynamic fusimotor neurones while the modulated type was due to static fusimotor neurones.

4. The patterns of fusimotor activity seen in these rhythmic movements under light anaesthesia agree well with the patterns deduced from spindle recordings in the conscious cat during mastication.

5. The results emphasize the importance of looking beyond a simple hypothesis of 'α-γ co-activation' to explain fusimotor function. It is proposed that tonic dynamic fusimotor activity is set at the beginning of a movement to determine the incremental sensitivity of primary endings to stretch. The static fusimotor fibres are activated principally during shortening to help keep both primary and secondary endings active.

INTRODUCTION

The existence of separate static and dynamic fusimotor systems to the spindles of mammalian muscles offers various possible strategies for the use of the spindles in movement control (see e.g. Matthews, 1972).

Attempts to find out which strategy is actually used in a given movement can only be meaningful when normal movements are studied without the disturbance of anaesthesia. Such attempts have concentrated in recent years on recording from muscle spindle afferents. Thus Hagbarth & Vallbo (1969) introduced unit recording from human nerves and workers with this technique have generally emphasized a tendency for 'α-γ co-activation' (see Granit, 1970). In the special situation of rhythmic movements of the jaws in the cat (Taylor & Cody, 1974; Cody, Harrison

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& Taylor, 1975) and monkey (Goodwin & Luschei, 1975) and in locomotor movements of the cat hind limb (Prochazka, Westerman & Ziccone, 1977; Loeb & Duysens, 1979), the evidence has been in favour of more independent activation of the α and fusimotor system. It has been difficult to go beyond such rather general statements about fusimotor action, particularly regarding the roles of the static and dynamic components, because of the complex interactions of these with displacement and velocity in determining spindle afferent discharge. The need exists therefore to obtain direct recordings from identified fusimotor neurones during normal movements. Some progress in this direction has been reported by Lund, Smith, Sessle & Murakami (1979) who succeeded in recording the action of fusimotor neurones of jaw closing muscles in monkeys during isometric biting tasks. We now report a study of fusimotor action in the masseter nerve of the lightly anaesthetized cat in which we believe we have been able to identify separately the activity patterns of static and dynamic fusimotor axons. Though these movements are to some extent disorganized by the anaesthetic the results are generally consistent with our previous observations of spindle behaviour in conscious animals. An abstract of some of these results has appeared previously (Appenteng, Morimoto & Taylor, 1979).

METHODS

A total of twenty-seven cats were used in the weight range 2–3·9 kg. They were initially anaesthetized with pentobarbitone (36 mg/kg I.P.) and supplementary doses of thiopentone (10 mg/ml. I.V.) given when necessary. Tracheal, venous and bladder catheters were inserted and rectal temperature monitored. Pairs of enamelled silver wires, with their terminal 10 mm bared, were inserted into the masseter and digastric muscles for e.m.g. recording. Jaw movements were recorded using the compliant strain-gauge described previously by Taylor (1969).

Motor fibre recordings

Natural intramuscular nerve filaments of the masseter muscle were carefully teased apart from the surrounding muscle and recordings of functionally isolated single motor fibres were made from the cut central ends of such filaments. A bipolar electrode of interpolar distance 1 mm was employed. Conduction velocities of individual units were obtained either by means of stimulating down a glass-coated tungsten electrode implanted in the motor nucleus (Mot V) of the fifth nerve (impedance = 1 MΩ at 50 Hz; pulse duration = 0·1 msec, 0·5–2 V) or by an averaging technique.

The former approach was employed in ten animals and in these the motor nucleus was located using the procedures previously described by Appenteng, O'Donovan, Somjen, Stephens & Taylor (1978). Conduction length from the recording sites in the periphery to the point of exit of the fifth nerve from the brain stem was measured post mortem. A further 5 mm was allowed as the distance between this point and the motor nucleus (Berman, 1968), giving an over-all conduction distance of 49–57 mm (mean = 52 mm). In seven animals, conduction velocities were estimated by the 'back-averaging' technique originally described by Kirkwood & Sears (1975*a*, *b*). This involved triggering off the naturally firing unit spike recorded from the cut central end of an intramuscular filament and averaging the neurogram recorded by a bipolar electrode (interpolar distance = 1·5 mm) placed round the main trunk of the masseter nerve. The neurogram was digitally delayed by 3 msec (Medelec SD6) and averaging performed using a Medelec DAV6 module. The conduction distance between the two pairs of electrodes ranged from 8 to 12 mm and the conduction time was taken as the interval between the onset of the trigger-spike and the onset of the back-averaged response.

Spindle afferent recording

Following the initial surgery, animals were transferred to a stereotaxic frame and the mesencephalic nucleus of the fifth nerve (Me V) located in the manner described by Cody, Lee & Taylor (1972). Spindle afferents in the nucleus were identified on the basis of their response to passive movements of the jaw and to gentle probing. They were further classified according to their dynamic index and some units were also tested with an I.V. infusion of succinylcholine (dose 200 μg/kg).

RESULTS

Properties of efferent fibres in the masseter nerve

In the first series of observations the conduction velocity of axons in the masseter nerve was estimated by stimulating within Mot V. In any given fine filament of the nerve one or more all or none spikes could be distinguished by graded stimulation. The distribution of conduction velocity of 139 of these, shown in Fig. 1*A*, ranged from 9·1 to 95 msec^{-1}. This population should contain both alpha-motor and fusimotor fibres and presumably also some afferents whose central terminations in Mot V were excited, i.e. muscle spindle afferents making monosynaptic connexions (Appenteng *et al.* 1978). Conduction velocities of such spindle afferents (primary and secondary) estimated in other experiments (L. Harrison, J. Stephens & A. Taylor, unpublished observations) by stimulating masseter nerve and recording in Mes V are shown in Fig. 1*B*. Their lowest conduction velocity was 44 msec^{-1}. Those units included in Fig. 1*A* which were clearly identified as spontaneously active or excited by jaw opening are replotted in Fig. 1*C*. These are presumably all efferent and it is evident that the faster ones conduct within the speed range of the spindle afferents, while a few are even faster.

The small number of results in Fig. 1*C* relative to Fig. 1*A* is due to the fact that even very small filaments containing single naturally firing units often gave multiunit responses to central stimulation, so that it was uncertain which centrally excited unit corresponded to the naturally firing one. Completely specific identification was however possible by the technique of 'back-averaging' (Kirkwood & Sears, 1975*a*, *b*). An example is shown in the inset of Fig. 2. Here the spikes of a spontaneously firing unit recorded from the cut end of a filament (upper trace) triggered the averager, whose input was the neurogram recorded from the whole masseter nerve. The proximal electrodes of each pair were separated by 9 mm and the time difference between equivalent parts of the action potentials (marked by vertical lines in the Figure) was 0·33 msec, giving a conduction velocity of 27 msec^{-1}. The conduction velocities of twenty-one additional units estimated in this way are added to those of Fig. 1*C* in Fig. 2. There is thus no evidence for clear separation of two populations of masseter efferents corresponding to the α and γ groups of hind limb muscle nerves (see Boyd & Davey, 1968) and separate populations of fibre diameter (Eccles & Sherrington, 1930). It seems likely that fusimotor fibres of masseter nerve would have conduction velocities in the lower end of the distribution, but they cannot be identified on this basis alone and some additional physiological criteria are needed. It should be pointed out that the motor fibres examined were those which were spontaneously active or which responded to muscle stretch, and some fusimotor units and high threshold α motor fibres would have been neglected.

Examined by passive stretch of the muscle the efferent fibres did fall into two groups. In Fig. 3*C* (insert) is shown an example of a unit normally silent with the jaw closed but excited at 26 impulses sec^{-1} by muscle stretch, behaviour appropriate for an α-motor unit excited by the stretch reflex. By contrast, the unit shown in Fig. 3*D* had a resting discharge of 13 impulses sec^{-1} which increased only very

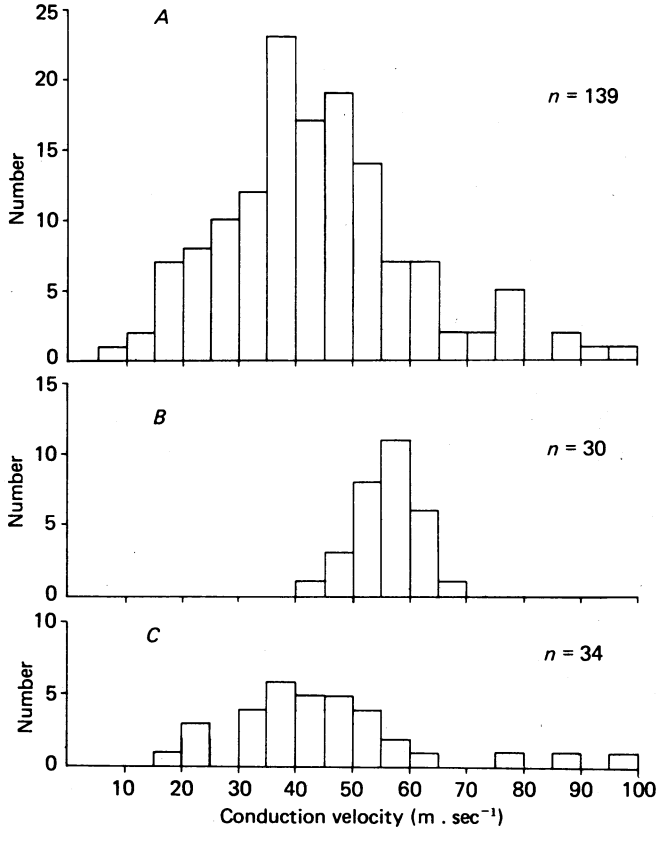

Fig. 1. Histograms of unit conduction velocities obtained by central stimulation. *A*: all units. *C*: identified motor fibres. *B*: spindle afferents; see text.

slightly during stretch (up to 16 impulses sec^{-1}). Units responding by no more than 5 impulses sec^{-1} to such stretch have been designated as stretch insensitive and those responding by more than this as stretch sensitive. In Fig. 3*A* is shown the relationship of stretch sensitivity to conduction velocity. Of the thirty-two stretch sensitive units, all but two had conduction velocities above 35 msec^{-1} while of the twenty-three stretch insensitive units all but five had conduction velocities below 35 msec^{-1}. Fig. 3*B* shows that resting discharge frequency and conduction velocity and stretch sensitivity were related. Thus all the stretch insensitive units had resting frequencies in excess of 11 impulses sec^{-1} whereas only three out of sixteen of the others had resting discharge above this frequency, indeed nine of them were normally silent.

In summary then, it was found that in one part of the masseter efferent population

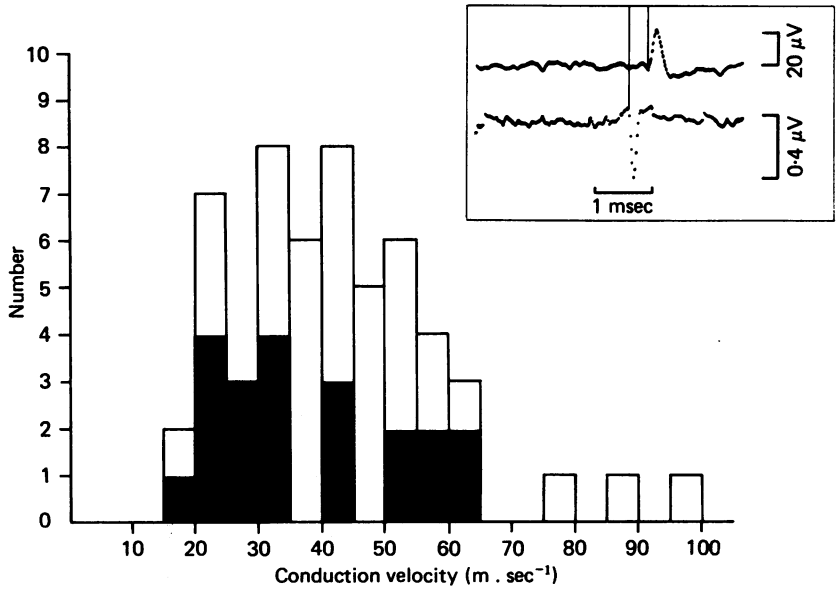

Fig. 2. Histogram of motor fibre conduction velocities (n = 55) obtained by 'back-averaging' (filled bars, n = 21) or by central stimulation (n = 34). Inset: estimation of conduction velocity by 'back-averaging' method. Top trace shows unit spike delayed by 3 msec and lower trace averaged neurogram recorded more proximally from main nerve trunk and delayed in the same way. Both traces are the average of 1024 sweeps.

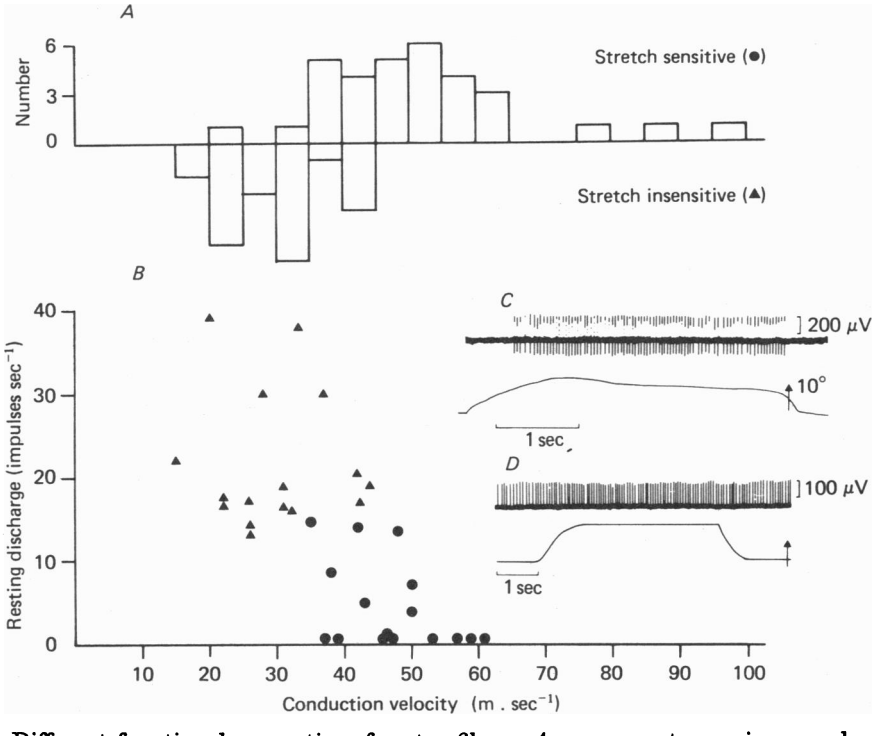

Fig. 3. Different functional properties of motor fibres. *A*: response to passive muscle stretch. *B*: spontaneous discharge rate. Note that most units with conduction velocities below 35 msec^{-1} are stretch insensitive and have high resting discharges (presumed fusimotors). Inset: original records from a stretch sensitive (*C*) and stretch insensitive (*D*) unit.

there was an association of conduction velocity below 35 msec^{-1}, insensitivity to muscle stretch, and a resting discharge of more than 11 impulses sec^{-1}. In the rest, conduction velocity was above 35 msec^{-1}, firing was caused or greatly increased by stretch and resting discharge was zero or less than 11 impulses sec^{-1}. We therefore propose to regard the former as fusimotor and the latter as alpha-motor responses. In support of this conclusion it was found that fusimotor type responses were only obtained from nerve filaments supplying the anterior part of masseter and not from ones supplying the posterior part and this corresponds to the concentration of spindles in the anterior part of the muscle found by Lund, Richmond, Touloumis, Patry & Lamarre (1978).

Natural stimuli in and around the mouth commonly affected the fusimotor firing. Thus lightly stroking the hairs of the submandibular skin caused increased firing up to 30 impulses sec^{-1} in all of six units tested. Light pressure on canine teeth usually inhibited firing, sometimes specifically for a particular direction of pressure. Brushing the dorsum of the tongue also commonly reduced fusimotor firing.

Fusimotor behaviour during reflex movements

As reported by Taylor & Davey (1968) it is possible to induce cyclic jaw movements in the anaesthetized cat by placing fluid, particularly dilute alcohol, in the mouth. A light level of anaesthesia is essential such as is achieved about 3 h after an initial dose of 30 mg/kg sodium pentobarbitone I.P. Maintenance doses of thiopentone were given as necessary to prevent shivering or spontaneous limb movements. It was desirable to reduce noxious stimuli as far as possible, for example from the head clamp, to which end a plate screwed to the skull was substituted for the usual clamp.

The cyclic jaw movements observed could be as much as 20 degrees in extent and repeating at up to 2 per second, commonly for 3–4 cycles or for longer, at lower frequencies. On many occasions the movements most resembled those of lapping (see Taylor & Cody, 1974), having the opening phase slower and more prolonged than the closing phase.

Satisfactory recordings were made from a total of twenty-four units presumed to be fusimotor on the above criteria, together with jaw movements in sixteen animals. Two main types of behaviour were observed. In six units there was an increase in firing frequency on placing fluid in the mouth. The increase started before jaw movements commenced and was maintained with only small and irregular fluctuations during the ensuing movements. Examples of this are shown in Fig. 4. The unit in A starts at 27 impulses sec^{-1}, increases smoothly to 44 impulses sec^{-1} before the first movement cycle and remains at an elevated level during the whole sequence of movements. It is seen that the irregularity of discharge also increases and that there is some slight fluctuation in frequency related to the movements. These fluctuations take the form of small increases in frequency starting before each movement but without any detailed relation to the phases of opening and closing. The enhancement of this fusimotor firing precedes the onset of masseter e.m.g. by some two seconds and throughout the record remains elevated irrespective of interruption of e.m.g. activity. Fig. 4*B* shows similar behaviour of another fusimotor

fibre during a rather different movement pattern. Discharge again increases definitely before the first movement, this time from 13 to 62 impulses sec^{-1}. The small enhancements seen related to the first three closing movements do not recurr subsequently. This type of behaviour will be referred to as 'sustained'.

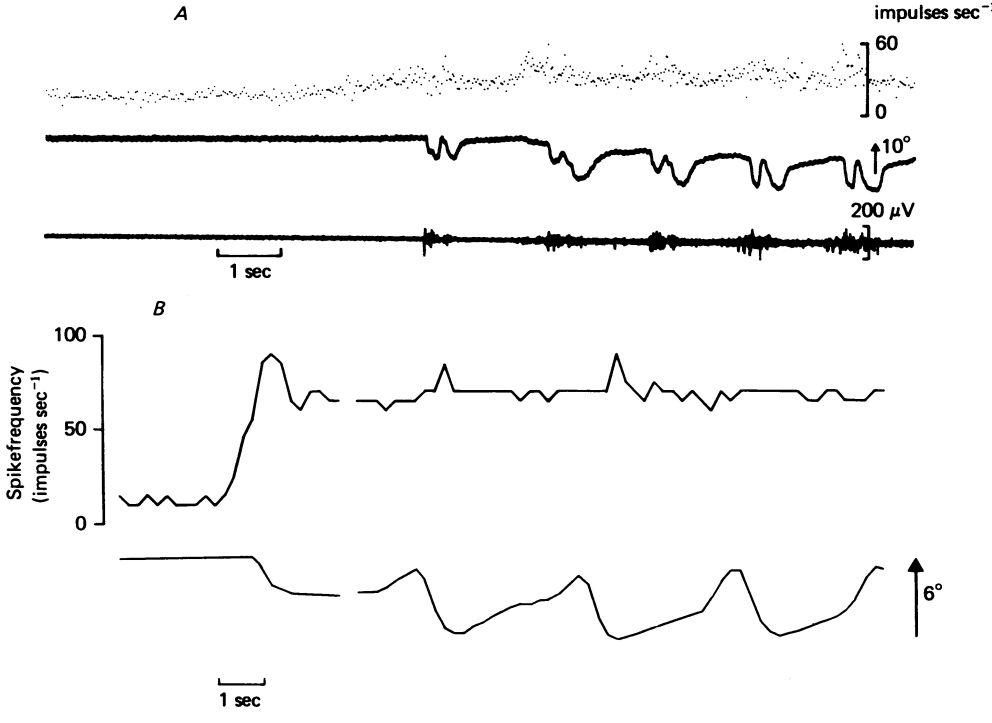

Fig. 4. Two fusimotor fibres (*A*, *B*) showing 'sustained' pattern of behaviour during reflex movements. Note enhancement of discharge prior to initial movement and that fluctuations in firing during movements are not well related to displacement or e.m.g.

The other main pattern of fusimotor discharge seen in fifteen cases is illustrated in Fig. 5*B* and *C*. Here there is no general increase during movements, but rather a striking phasic modulation of frequency. Notice that the frequency increase leads the masseter shortening movement. The fusimotor discharge does not always accompany the muscle shortening but commonly in the first part of a movement sequence may be silenced, as in this case. This type of behaviour will be called 'modulated'. There is a more direct relationship between the behaviour of this type of unit and alpha motor activity than in the case of the sustained type. Even here however, the association is rather variable. Thus in Fig. 5*C*, at the earliest phases of the developing movement pattern there is fusimotor acceleration from 16 to 54 impulses sec^{-1} with no e.m.g., followed by acceleration to 80 impulses sec^{-1} in the presence of a large e.m.g. burst. Also the fusimotor unit was silenced once for 0·5 sec when there was some low amplitude e.m.g. present. Examination in detail of the increments in fusimotor firing and the associated movements, showed no significant correlation in this record. Nevertheless when a large burst of e.m.g. accompanied a rise in fusimotor firing the two were very closely related temporally.

A striking feature of the fusimotor firing is its range of modulation. Thus in Fig. 5*B* smoothly increasing discharge occurred up to 135 impulses sec^{-1} in contrast to the alpha motor unit spikes in the e.m.g. which were recruited at about 40 impulses sec^{-1} and showed little if any frequency modulation.

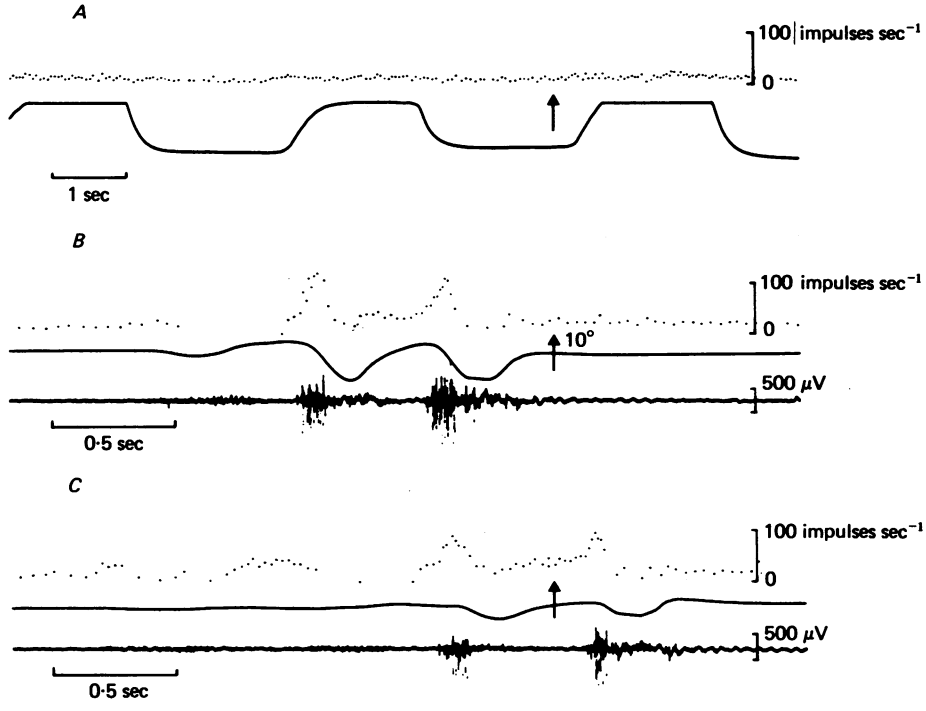

Fig. 5. Fusimotor fibre displaying 'modulated' pattern of behaviour. *A*: effect of passive muscle stretch. *B* and *C*: discharge during reflex movements. Note enhancement some 0·1 sec before muscle shortening but that firing also shows some independence over e.m.g. activity (*C* and initial closure in *B*).

In addition to these two main types, two of the units characterized as fusimotor showed no change in frequency with reflex jaw movements and one showed bursts of firing at 40 impulses sec^{-1}, apparently related to respiration.

Changes in spindle behaviour during reflex jaw movements

With regard to the main classes of fusimotor behaviour described above, the question arises as to whether they may be identified with separate action in static and dynamic 'γ' efferents. No means was available for distinguishing individual fusimotor fibres as static or dynamic during the present experiments. We have therefore tried to see whether changes in spindle behaviour occur during reflex jaw movements which could be explained on the basis of each fusimotor class being recognized as static or dynamic.

A total of twenty-two spindle first order afferents were recorded from their cells in Me V as described by Cody *et al.* (1972), with the usual stereotaxic head clamps replaced by a plate screwed on the skull. The mandible was either free to move or

was attached to a servo puller moving sinusoidally at 1 Hz and 1·5 degrees amplitude. The conditions of anaesthesia were closely similar to those described above. The responses of eleven of these units were tested with ramp stretches before and after I.V. succinyl-choline and 6 designated as from primary endings and five from secondary endings by the criteria of Cody *et al.* (1972).

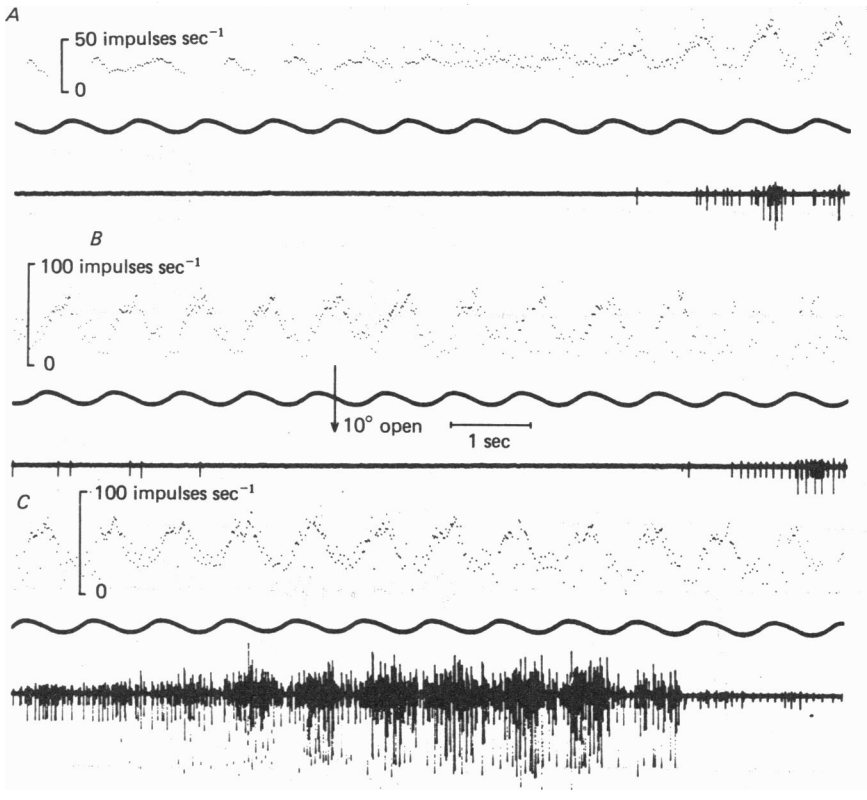

Fig. 6. Continuous record of changes in discharge of masseter spindle primary in response to tail pinching, during application of constant amplitude sinusoidal stretching. The static (*A*) and dynamic (*B*) sensitivities of afferent can alter independently of e.m.g.

Fig. 6 shows the behaviour of a masseter primary spindle afferent with constant sinusoidal stretch and the effect of non-specific arousal by tail squeezing. Initially the firing was mostly during the lengthening phase, with variable periods of following throughout the cycle. There was relatively little irregularity of firing and the peak to peak modulation (when not silenced during shortening) was 13 impulses sec^{-1} and the mean 28·5 impulses sec^{-1}. On arousal, the discharge became more irregular and the mean frequency rose to 35 impulses sec^{-1}. Firing was now consistently throughout the cycle and there was no obvious modulation. Then after about 3 sec, modulation increased progressively to 52 impulses sec^{-1} with a mean of 39 impulses sec^{-1}. In Fig. 6*C*, further tail pinching led to a rise in mean frequency to 53 impulses sec^{-1} with modulation unchanged, and a vigorous stretch reflex in masseter ensued. These changes are most readily interpreted as being due to an initial increase in

static fusimotor drive (*A*) followed by increased dynamic fusimotor action (*B*) and perhaps a further enhancement in static action in *C*. Evidently this preparation can display separate activation of the two types of fusimotor fibre. Other spindle units tested by putting fluid in the mouth showed similar evidence for separate enhancement of static and dynamic drive. These recordings also make it clear that there need be no rigid relationship between the α-motor and fusimotor activity.

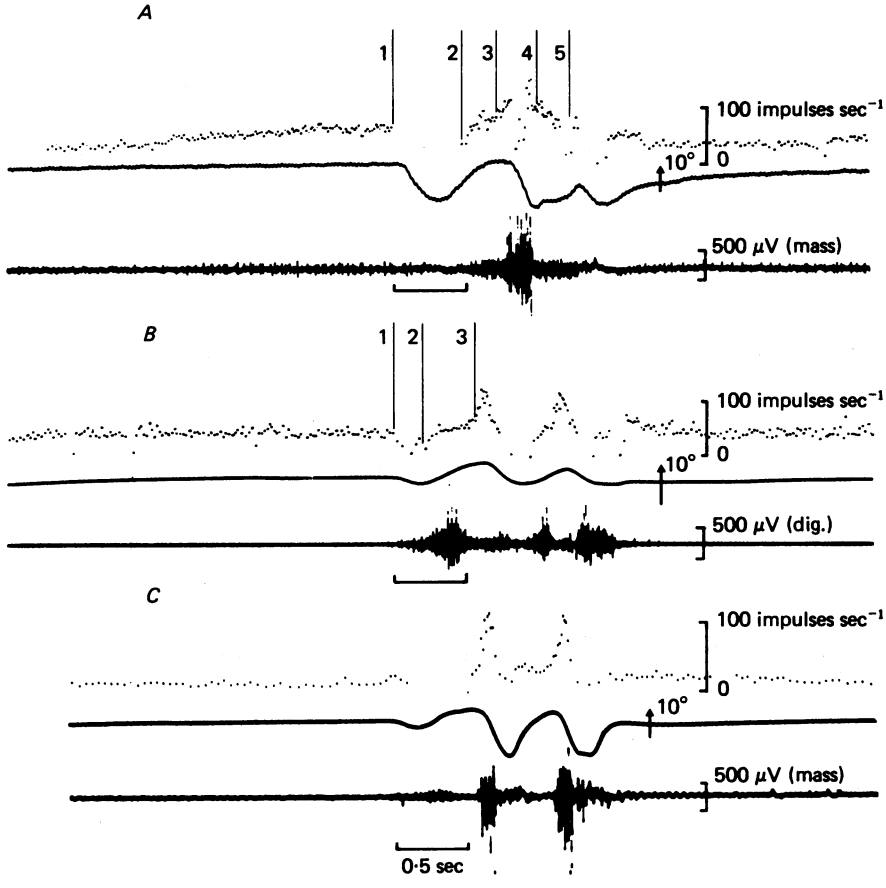

Fig. 7. Different behaviour of primary (*A*) and secondary (*B*) spindle afferents. Note that whilst only the primary shows enhancement of discharge before initial movement, both afferents can show enhancements some 0·1 sec before muscle shortening (three in *A* and *B*). *C*: fusimotor fibre of Fig. 5*B*.

In the situation in which the animal's jaw was free to move in response to fluid placed in the mouth, spindle firing also showed changes indicating modification of fusimotor drive. Fig. 7*A* for example indicates that about 2 sec before any length change, a spindle primary afferent increased its firing smoothly from 24 to 65 impulses sec^{-1}. This could have resulted from either static or dynamic fusimotor action, but it seems more likely to have been due to dynamic because the spindle was totally silenced immediately at the onset of active shortening (1), which is not expected with a background of static fusimotion. The spindle remained silent

throughout shortening and only resumed firing (2) when the length had returned about half-way to its starting value. Firing then continued to increase roughly in parallel with length but then after maximum length had been reached (3) showed a further marked increase in firing, this occurring some 0·1s before the onset of shortening. Firing was interrupted briefly at the onset of shortening, but resumed, to reach a maximum of 150 impulses sec^{-1} during the phase of rapid shortening.

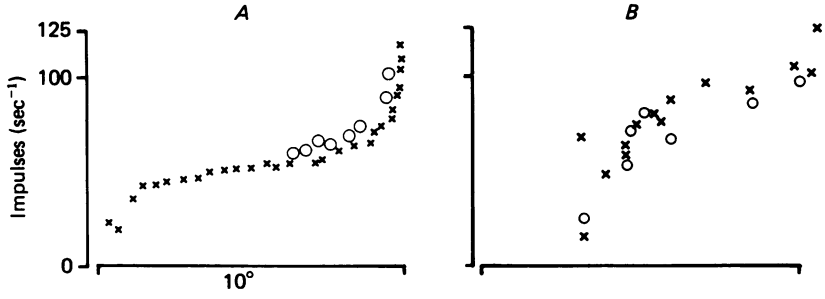

Fig. 8. *A*: plot of instantaneous firing frequency against jaw opening for secondary afferent shown in Fig. 7*B*. *B*: plot for secondary afferent in normally behaving animal – see text. Symbols, crosses indicate muscle stretch and circles muscle shortening. Muscle lengthening to the right.

Finally the afferent frequency declined smoothly during the period (4–5) when muscle length was approximately constant. The events between 3 and 4 can best be explained by a brief period of increased static fusimotor activity dying away in 4–5. The afferent burst is interrupted briefly by the onset of rapid shortening, but is then resumed and reaches its maximum actually during shortening.

Confirmation of this interpretation comes from a record of a spindle secondary afferent, in Fig. 7*B*, which is expected to show only static fusimotor effects. Notice that there is no change in frequency before the movements begins (1), thus supporting the conclusion that the early increase in Fig. 7*A* is due to dynamic action. A smooth rise in frequency parallels lengthening in the period 2–3 but there is a marked burst of some 50 impulses sec^{-1} at the peak of lengthening when the muscle is at constant length. Note that as in Fig. 7*A* (3) this increase occurs some 0·1 sec before the onset of shortening. This is repeated for the second cycle. In both cases firing falls fairly smoothly with shortening.

Such behaviour was a consistent feature in these conditions therefore, though obtained on another occasion the fusimotor record of Fig. 5*B* is shown for comparison in Fig. 7*C*. The form of the fusimotor discharge relative to the spindle secondary firing adds strong circumstantial evidence that the former is likely to have been from a static fusimotor fibre.

An instructive way of presenting spindle activity is to plot instantaneous frequency as a function of length as in Fig. 8. In *A* we see that the secondary unit of Fig. 7 after the first two impulses shows a roughly linear relation of frequency to length during the stretching phase until almost maximum length is reached. There is then a sudden increase in firing with very little length change, which is interpreted as due to a static fusimotor burst. Firing frequency then falls along a trajectory very similar to the rising one, but not continuing so far. The plot of Fig. 8*A* can be

compared conveniently with that of Fig. 8*B* taken from the data of Cody *et al.* (1975) from the conscious cat making eating movements. The chief differences are that in normal movements there is no extra increase in frequency of the secondary endings at the end of lengthening, and that firing continues down to the shortest lengths. The difference could be explained if during light anaesthesia the static fusimotor burst starts earlier and finishes earlier relative to the movement than in the normal.

DISCUSSION

The jaw muscles in the cat are interesting for studies of motor control because of the relative simplicity of their action and the possibility of recording from both afferents and efferents during normal movements. It is important in such studies however not to transfer information obtained from hind-limb observations to the jaw muscles without careful checking. For example there is no evidence that jaw muscle spindle primary and secondary afferents can be separated reliably by conduction velocity (Appenteng *et al.* 1978) nor are the α-motor and fusimotor axons completely separate on this basis alone. It may be that the short conduction distances involved have not favoured the evolution of well separated fibre diameters related to function.

For these reasons we have supplemented conduction velocity measurements of motor axons with other tests to distinguish fusimotor from α-motor activity. We found there to be an association in one group of efferents of low conduction velocity, relatively high resting discharge frequency, insensitivity to muscle stretch and marked sensitivity to skin stimulation. There can of course be no certain identification of a fusimotor neurone without a demonstration of its effects on spindle firing in the absence of extrafusal contraction. However, by analogy with lumbro-sacral (Matthews, 1972) and intercostal muscles (Sears, 1964; Eklund, Euler & Rutkowski, 1964), it seems reasonable to believe that this group is indeed fusimotor. Although we have no evidence regarding the existence of 'β' innervation in the jaw muscles, our fusimotor group will presumably exclude beta fibres as they would be expected to show the same reflex excitation from muscle stretch as do alpha-motoneurones (see Burke & Tsairis, 1977).

Some data does already exist regarding the identification of α and fusimotor neurones of the jaw elevator muscles. Thus Sessle (1977) recorded extracellularly from masseter and temporalis motoneurones in Mot V. The stated criteria for recognition of 'γ' motoneurones were a low conduction velocity, absence of monosynaptic excitation on stimulation of Mes V (largely elevator spindle afferent somata) and the presence of a spontaneous discharge. However, as only 45 % of the presumed γs showed spontaneous firing and only 82 out of 205 masseter and temporalis motoneurones were tested for monosynaptic excitation, it is clear that some motoneurones were classed as gammas solely on the basis of their conduction velocity. The conduction velocity range of those taken to be of γ type was 16–27 msec^{-1}, whilst the alpha conduction velocity range was 26–45 msec^{-1}, though most were within 26–45 msec^{-1}. By comparison our data give the conduction velocity range for presumed fusimotor fibres as 15–45 msec^{-1} and for αs as 20–95 msec^{-1}, with most αs between 25 and 65 msec^{-1}. In the recent study of Lund *et al.* (1979) on

the monkey, three motoneurones were classed as 'putative gammas' on the basis of lack of response to passive jaw movement. Two only were excited antidromically and had conduction velocities of 19 and 38 msec^{-1} compared with seven αs in the range 36–90 msec^{-1}. Periods of tonic firing with frequencies up to 200 impulses sec^{-1} were seen in the 'γs'.

Within the fusimotor group, identification of an individual axon as static or dynamic depends on observing the effect of stimulating it on a spindle's response to stretch. This is not possible when the axon is interrupted to permit recording from its central end, and so we can only attempt indirect identification. In the present work, fusimotor axons fell into two distinct groups regarding their activity patterns seen in the reflex response to oral stimulation. One group showed a sustained increase during cyclic movements, whereas the other showed strongly modulated behaviour. This is reminiscent of the continuous tonic action and phasically modulated action of different fusimotor axons seen in the intercostal nerve filaments (Sears, 1964; Eklund *et al.* 1964). The question which arises is whether these two patterns correspond to activity in the two types of fusimotor fibre. Corda, Euler & Lennerstrand (1966) showed that in decerebrate cats, the rhythmic gamma spikes in intercostal filaments disappeared after high spinal transection, but that the tonic γ spikes remained. The experiments of Alnaes, Jansen & Rudjord (1965) indicated that spinalization causes loss of spontaneous static fusimotor activity in hind-limb nerves. Recently, by direct observation, Gladden & McWilliam (1977) showed that activity in nuclear chain fibres, present in the lightly anaesthetized preparation, disappeared after cutting the cord. We may conclude that the rhythmically active intercostal fusimotors are probably gamma static. In the present results the evidence is also in favour of the modulated fusimotor activity, in masseter nerve, being in static fibres.

On the other hand, the tonic intercostal units which persisted after spinalization were probably dynamic because the predominant fusimotor activity to hind-limb muscles after spinalization is seen to be dynamic (Alnaes *et al.* 1965; Gladden & McWilliam, 1977). This is consistent with the conclusion reached earlier that the sustained fusimotor discharges are due to dynamic fusimotor neurones.

In the work of Sjostrom & Zangger (1976) on the spinal cat treated with L-DOPA to excite fictive locomotion, fusimotor discharge seemed to parallel the alpha activity. For flexor muscles, the evidence of Bergmans & Grillner (1968, 1969) suggests that this was static fusimotor activity. Sjostrom & Zangger also suggest, on the basis of the work of Bergmans & Grillner (1968, 1969) that in the extensor muscles, γ dynamic fibres were also co-activated. However, in their specific experiments there was no direct evidence to this effect. Indeed as the behaviour of their extensor spindle afferents (compare Fig. 4 with Fig. 2) differed from that of the flexors, this suggests that dynamic fusimotor fibres have a different pattern from the statics.

A well known hypothesis regarding the way in which the fusimotor system is used is that it is 'co-activated' with the α motoneurones of a particular contracting muscle (for review see Granit, 1970). The rationale of the proposal is that it might ensure continued activity of spindle afferents during active muscle shortening so that negative feedback control is not interrupted, when it may be most desirable to retain it. However, although parallel firing of α and γ motoneurones is often

known to occur, the usefulness of the concept is limited (as pointed out by Matthews, 1972) by confusion as to whether 'α-γ co-activation' should be taken to imply a simple experimental observation of parallel function under some conditions or the existence of a more or less fixed neural connexion between the two systems. Another deficiency of the α-γ co-activation hypothesis is that it makes no distinction between the action of the static and of the dynamic fusimotor systems though 'there can no longer be any doubt that if and when it so requires, the central nervous system can activate static and dynamic fusimotor neurones largely independently of each other' (Matthews, 1972, p. 528).

Most of the evidence for this conclusion relates to studies with electrical stimulation of central structures. The present work goes a little further to show the generality of the potential independence of γ static, γ dynamic and α motor activity in the specific situation of reflex jaw movements in the lightly anaesthetized cat. The question which arises is how well do the presently observed patterns of action represent the normal organization in unrestrained and unanaesthetized animals? From experiments on hindlimb and tail muscle spindles of the normal cat (Prochazka, Stephens & Wand, 1979) there is some indication that static fusimotor discharge can vary during movements, though A. Prochazka (personal communication) interprets recordings from secondary afferents to indicate a constant tonic static action throughout cyclic movements. This conclusion is based on the observation of a constant relation of firing frequency to length during lengthening and shortening as also found for jaw muscles by Cody *et al.* (1975). The alternative explanation, which we prefer, is that such a result may be achieved by phasically enhanced static drive during shortening. Indeed the firing pattern of primary endings in conscious animals can show marked dynamic sensitivity during lengthening (see Fig. 1, Prochazka *et al.* 1979) compared with passive movements which is not compatible with a strong tonic static drive persisting into this phase of active movement (see Fig. 8, Hulliger, Matthews & North, 1977). This would be most simply interpreted as showing the existence of dynamic action during the period when α firing is minimal, and is compatible with continued dynamic fusimotion throughout the cycle.

Human experiments indicate that static fusimotor activity is generally closely related to extra-fusal contraction (Vallbo, 1974*b*; Burke, Hagbarth & Lofstedt, 1978), whereas dynamic effects can be seen to be enhanced tonically in spindles of muscles not directly involved in the contraction (Burg, Szumski, Struppler & Velho, 1976).

The present results are of immediate relevance to the earlier study of Cody *et al.* (1975) who have compared the behaviour of jaw elevator spindle afferents in normally behaving cats to that in deeply anaesthetized animals with fusimotion suppressed by pentobarbitone supplemented by chlorpromazine. In the latter case, previously recorded natural eating movements were reproduced exactly by a servo device. For active masticatory movements the discharge of presumed spindle secondaries bore a close relationship to the muscle length during both jaw opening and closing. In passive movements, spindle secondaries silenced on muscle shortening but on muscle lengthening (jaw opening) their length sensitivity was essentially the same as that observed in active movements. The conclusion drawn was that 'static fusimotor

drive can be low or absent during the muscle lengthening phase and yet be enhanced during shortening': this is entirely compatible with the pattern of the presumed static fusimotor discharge described in the present results. For their sample of presumed primaries, the significant change in behaviour with fusimotion suppressed was a marked reduction in the maximum instantaneous frequencies during passive muscle lengthening. This was taken as evidence for the presence of dynamic fusimotion during active movements. Thus there is evidence for jaw movements both in the conscious and in the lightly anaesthetised cat, that the dynamic fusimotor system may be active tonically throughout cyclic movements while the static fusimotor neurones discharge mainly during active shortening. Nevertheless, the detailed relationship of static fusimotor to alpha motor firing *does* appear to be disturbed during anaesthesia. In the normal animal the spindles did not usually accelerate during active shortening, though this did happen commonly (as seen in Fig. 7*A* and *B* and Fig. 8*A*) during light anaesthesia. Since the disturbance affected both primary and secondary endings it seems likely to be due to a disturbance of the timing of the modulated static fusimotor discharge relative to shortening. It appears that a properly timed static fusimotor burst during muscle shortening may be able to ensure that the secondary afferents at least continue to indicate length quite reliably during the shortening phase as well as during lengthening, which is not the case during passive movements of the jaw without fusimotor activity (Cody *et al.* 1975). A generalization may be proposed therefore, as the basis for future investigations, that the dynamic fusimotor system acts tonically during movements to set the incremental sensitivity of primary endings to stretch. The static fusimotor fibres are activated principally during muscle shortening to help keep both primary and secondary endings active and to take up slack in the intrafusal fibre so that discharge rises smoothly again directly lengthening begins. The static fusimotor fibres would so to speak reset the operating zero point at the end of each active shortening. Other strategies for the use of the fusimotor system are no doubt possible, but this proposal may be worth serious consideration as an alternative to the ideas of length follow-up servo action, α-γ co-activation or the separate regulation of length and velocity feed-back all of which have turned out to have serious deficiencies.

This work was supported by the Research Endowment Fund of St. Thomas's Hospital and in part by the Medical Research Council.

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