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

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SUMMARY

1. Simultaneous recordings were made from fusimotor axons in the central ends of filaments of the masseter nerve, and from masseter and temporalis spindle afferents in the mesencephalic nucleus of the fifth cranial nerve in lightly anaesthetized cats.

2. Fusimotor and α-motor units in the masseter nerve were differentiated on the basis of their response to passive ramp and hold stretches applied to the jaw. Spindle afferents were identified as primary or secondary according to their dynamic index after administration of suxamethonium.

3. The activity of a given fusimotor unit during reflex movements of the jaw followed one of two distinct patterns: so-called 'tonic' units showed a general increase in activity during a movement, without detailed relation to lengthening or shortening, while 'modulated' units displayed a striking modulation of their activity with shortening, and were usually silent during subsequent lengthening.

4. Comparison of the simultaneously recorded fusimotor and spindle afferent activity suggests that modulated units may be representative of a population of static fusimotor neurones, and tonic units of a population of dynamic fusimotor neurones.

5. In these lightly anaesthetized animals, both primary and secondary spindle afferents showed increased firing during muscle shortening as well as during lengthening. This increase during shortening is not usually seen in conscious animals and reasons are given for the view that it is due to greater depression of α-motor activity than of static fusimotor activity during anaesthesia.

6. The results are discussed in relation to the theories of 'α–γ co-activation' and of 'servo-assistance'; and it is suggested that static fusimotor neurones provide a 'temporal template' of the intended movement, while dynamic fusimotor neurones set the required dynamic sensitivity to deviations from the intended movement pattern.

INTRODUCTION

In order to understand the part played by the fusimotor system of mammals in controlling voluntary movement, it is desirable to know the patterns of discharge in static and dynamic fusimotor neurones during a variety of normal movements. Considerable progress has been made in deducing these patterns from recordings of spindle afferent firing during natural movements in the case of jaw movements in

the cat (Taylor & Cody, 1974; Cody, Harrison & Taylor, 1975) and monkey (Matsunami & Kubota, 1972; Goodwin & Luschei, 1975; Larson, Smith & Luschei, 1981) and the hind-limb movements of the cat (Prochazka, Stephens & Wand, 1979; Prochazka, Westerman & Ziccone, 1976, 1977; Loeb & Duysens, 1979). The general conclusions from this work are that fusimotor discharge cannot be regarded as the command signal because there is no net excitation of the afferents during muscle shortening as would have been required by the original 'length follow-up servo' theory (Merton, 1953). Neither is a simple co-activation of α- and fusimotor neurones (see Granit, 1970) adequate to explain the results, because there is much variability in the relation between spindle firing and muscle length changes. It has also become evident that static and dynamic fusimotor neurones have different central connexions and can indeed be selectively activated, thus making the general concept of 'α–γ co-activation' an obvious over-simplification (see Matthews, 1981).

Progress in all this work has been hampered by the difficulty in deducing quantitatively what changes are occurring in static and dynamic fusimotor neurones from the observed behaviour of primary and secondary spindle afferents. Recently, Prochazka & Hulliger (1983) have advanced the interpretation of such data by stimulating identified static and dynamic fusimotor fibres to cat hind-limb muscles in acute experiments to try to match spindle discharge patterns previously recorded with implanted electrodes in natural movements. Promising as this approach is, it would still be a great advantage to have direct recordings from identified static and dynamic fusimotor neurones. One possible approach to this has been the attempt by Lund, Smith, Sessle & Murakami (1979) to record from fusimotor neurones via metal micro-electrodes implanted in the motor nucleus of the fifth cranial nerve in monkeys. Unfortunately, experimental difficulties made this work rather unrewarding, but a less ambitious approach by recording from efferent fibres in the masseter nerve in lightly anaesthetized cats has at least started to show some of the characteristics of fusimotor firing during reflex movements of the jaw (Appenteng, Morimoto & Taylor, 1980).

The proper interpretation of such data requires firm identification of static and dynamic fibres, but this cannot be done by the classical approach of observing their effects on spindle afferent firing, because the efferents are inevitably interrupted. Instead, identification has been indirect by observing spindle afferent discharge in separate but similar experiments. In the present work we carry this a stage further, by recording spindle afferents and fusimotor efferents simultaneously. By so doing it has been possible to strengthen the previously expressed view that dynamic fusimotor activity provides a tonic background control of spindle sensitivity during movements. Static fusimotor discharge, however, seems to be strongly modulated with movement and it is proposed that this may form a 'temporal template' of the intended movements.

A preliminary account of this work has been presented to the Physiological Society (Gottlieb & Taylor, 1983).

METHODS

A total of sixteen male and female cats were used, in the weight range 1·5–3·5 kg. Anaesthesia was induced with sodium pentobarbitone (Sagatal, 60 mg/kg, I.P.) and maintained thereafter with sodium thiopentone (10 mg/ml, I.V.). Tracheal and venous cannulae were inserted, and the animal wrapped in a heated blanket. Pairs of enamelled silver wires, their terminal 10 mm bared, were inserted into the masseter and digastric muscles for e.m.g. recording. The electromyograms were full-wave rectified and smoothed (time constant 100 ms). Movements of the jaw were recorded with a light, compliant strain guage as described by Taylor (1969).

Application of passive stretch. A small stainless-steel screw was inserted into the mid line of the mandible, immediately ventral to the incisor teeth, so that a thin stainless-steel rod set into the head of the screw protruded from the mandible. The rod was attached to a displacement servo which was driven by a wave form generator. In the anaesthetized cat the mandible tends to assume a slightly relaxed position, corresponding to approximately 8·5° open at the temporo–mandibular joint. Units were tested with a standard 1·6° ramp and hold stretch (jaw opening), starting from this 'rest' position, and also by closing the jaw completely.

Motor-fibre recordings. The masseter nerve was exposed by removing the middle third of the zygomatic arch and splitting the underlying muscle. The pool thus made was filled with paraffin oil, and natural intramuscular filaments of the masseter nerve were teased apart from the surrounding muscle. Differential recordings were made from the cut central ends of such filaments with stainless-steel hook electrodes. The reference electrode was placed at the base of the filament. The fusimotor activity recorded in this manner, from cut filaments, was considered to be representative of the activity of intact fusimotor neurones in continuity with their intrafusal fibres.

Spindle-afferent recordings. After the initial surgery, the animals were transferred to a stereotaxic frame (La Précision Cinématographique), and a glass-coated tungsten micro-electrode with an impedance in the range of 1–3 MΩ at 1·7 kHz (Merrill & Ainsworth, 1972) placed in the mesencephalic nucleus of the fifth cranial nerve (for further details see Cody, Lee & Taylor, 1972). The cell bodies belonging to the spindle afferents from masseter and temporalis muscles were identified on the basis of their response to passive stretches of the jaw, and their muscle of origin identified by gentle probing. They were classified further as primary or secondary according to their dynamic index with suxamethonium (Scoline, 200 μg/kg, I.V.). Artificial ventilation was maintained for up to 10 min following administration of suxamethonium. After locating the mesencephalic nucleus of the fifth nerve, the electrode was secured by cementing the light Perspex chamber, in which it was housed, to the cranium with dental acrylic cement (for further details see Cody *et al.* 1975). The cat could then be removed from the stereotaxic frame, and the customary face clamp was replaced with a light metal plate screwed to the cranium. This conferred the considerable advantage that noxious input from the face was thereby reduced, making it easier to elicit reflex movements of the jaw.

RESULTS

Identification of fusimotor fibres in masseter nerve. Fusimotor and α-motor units were distinguished primarily on the basis of their characteristic responses to passive muscle stretches applied by opening the jaw, as illustrated in Fig. 1. The pattern of α-motor activity is represented by the masseter e.m.g., which is absent while the jaw is closed but strongly excited by opening the jaw. Stretch-induced activity of this sort is typical of α-motor units, excited by the stretch reflex of the jaw. Recordings from single units in the masseter e.m.g. and from efferents in the masseter nerve all show that α-motor units excited by stretch reach firing frequencies in the range 15–35 impulses/s. In marked contrast, the efferent in the upper trace maintains a tonic discharge of 35 impulses/s while the jaw is closed, and is unaffected by opening the jaw. Units of this sort were deemed to be fusimotor. It is recognized (Ellaway, Murphy & Trott, 1981) that some fusimotor neurones receive some multisynaptic autogenetic

facilitation from muscle stretch, therefore in keeping with Appenteng *et al.* (1980), efferent units which generally had the characteristics of fusimotor fibres were accepted as such provided that their increase in firing frequency during stretch was not greater than 10 impulses/s.

Satisfactory recordings were obtained from thirteen units classified as fusimotor on the above basis.

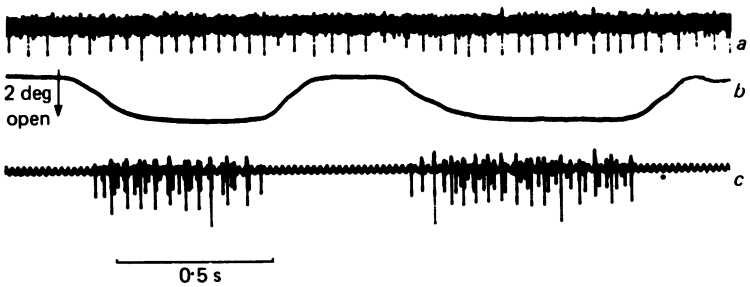

Fig. 1. Fusimotor and α-motor activity during passive stretching of the jaw-closing muscles. *a*, fusimotor; *b*, jaw displacement; *c*, masseter e.m.g. Lengthening of the jaw-closing muscles (opening) is represented by a downwards deflexion of the displacement record. The fusimotor unit is unaffected by stretch, in contrast to the α-motor units in the masseter e.m.g.

Motor and sensory fibres in hind-limb muscle nerves may be classified reliably on the basis of their diameter (Eccles & Sherrington, 1930) and conduction velocity (Boyd & Davey, 1968). However, attempts to do so for the masseter nerve, a branch of the mandibular division of the trigeminal nerve, have been unsuccessful. For example, Inoue, Morimoto & Kawamura (1981) identified spindle afferents in the mesencephalic nucleus of the fifth nerve as primary or secondary on the basis of their responses to stretch, vibration and suxamethonium, but found that the conduction velocities of these afferents showed considerable overlap. Subsequently, Morimoto, Inoue & Kawamura (1982) were able to measure afferent fibre diameters in the masseter nerve, having injected the trigeminal motor nucleus with kainic acid and caused the efferent population in the masseter nerve to degenerate. Although the afferent fibres were approximately bimodally distributed, a comparison of their diameters and conduction velocities indicated that both primary and secondary afferents would fall into the larger fibre diameter group (6–9 μm), and therefore could not have been distinguished on the basis of conduction velocity. Similarly, measurement of the conduction velocities of efferent fibres in the masseter nerve showed that, although functionally identified fusimotor units tended to have a lower conduction velocity than α-motor units, there was no evidence for a clear separation of α and γ populations (Sessle, 1977; Appenteng *et al.* 1980). Indeed, the estimated diameters of motor fibres in the masseter nerve were found to follow a unimodal distribution (Morimoto *et al.* 1982), indicating that trigeminal α- and γ-motor fibres may not be classified reliably on the basis of conduction velocity. In the present study therefore, conduction velocity measurements were not made.

Afferent fibres in masseter nerve. Six units recorded in the *central* ends of cut masseter nerve filaments were exquisitely stretch-sensitive, and responded with high-frequency bursts of activity when the masseter or temporalis muscles were gently probed. An

example of such a unit is shown in Fig. 2, during passive stretches applied to the jaw. Stretching the jaw-closing muscles excites the unit to 104 impulses/s, and it shows a modulation with the degree of stretch that is quite unlike the response of an α-motor unit. A small but appreciable dynamic component is also evident in the response, as the firing frequency has fallen to 82 impulses/s in the first 0·3 s of the hold phase of the stretch. Jaw closure then silences the unit completely. This particular unit was highly sensitive to probing the anterior part of the temporalis muscle, and was believed to be a spindle afferent from that muscle. Of the other units, one was thought to be a masseter spindle afferent, and four temporalis spindle afferents. Similar units have been reported in masseter nerve filaments by Kato, Kawamura & Morimoto (1982), who suggested that their presence in the central ends of cut masseter nerve filaments could be explained on the basis of branching by a parent axon to innervate more than one muscle spindle. If this explanation is correct, the above results would suggest that an axon can branch to innervate spindles in different closely related muscles (i.e. temporalis and masseter).

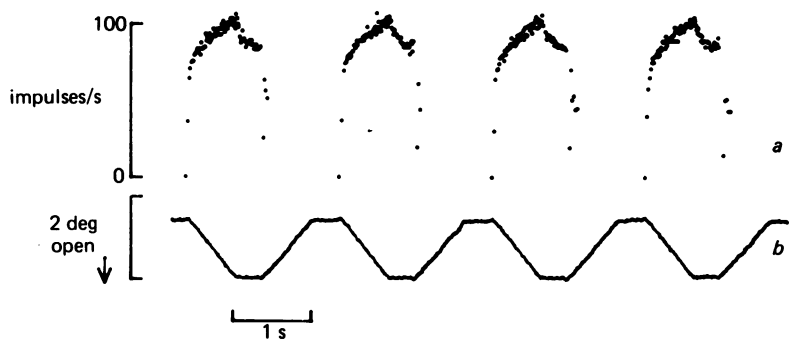

Fig. 2. Muscle spindle afferent activity in the central end of a cut masseter nerve filament. *a*, afferent; *b*, displacement.

Fusimotor activity during reflex movements. It is possible to elicit reflex movements resembling licking, swallowing and lapping in the lightly anaesthetized cat by placing fluid in the animal's mouth, as described by Taylor & Davey (1968) and Appenteng *et al.* (1980). It should be stressed that, although the level of anaesthesia was light, it was at all times sufficiently deep to prevent the animal shivering or making spontaneous limb movements.

Fusimotor activity during reflex movements of the jaw was clearly separable into two distinct patterns. Typical examples of both types are illustrated in Fig. 3. The unit shown in Fig. 3*A* displays little or no sensitivity to passive ramp and hold stretches, in keeping with its identification as a fusimotor unit, and maintains a modest firing rate in the range of 9–19 impulses/s. Subsequently, a reflex movement of the jaw was elicited, and the firing frequency of the unit can be seen to increase smoothly during the movement from some 20 impulses/s to a peak rate of 35 impulses/s. The frequency starts to increase about 0·25 s before the movement itself begins, and the peak frequency is achieved towards the end of the movement cycle, when the jaw is slowly returning to its 'rest' position. The major part of the movement is therefore accompanied by a smoothly increasing rate of fusimotor activity.

The unit in Fig. 3*B* similarly displays a negligible stretch sensitivity, maintaining a steady discharge in the frequency range of 9–26 impulses/s. However, it exhibits a different pattern of activity during a reflex movement: both closing phases of the movement are accompanied by a large and rapid increase in firing frequency from an initial rate, prior to the movement, of some 26 impulses/s and reaching a peak of 87 impulses/s. The unit is then momentarily silenced during the subsequent opening phases of the cycle. Note also that there is a brief increase of some 20 impulses/s in fusimotor firing frequency after the movement.

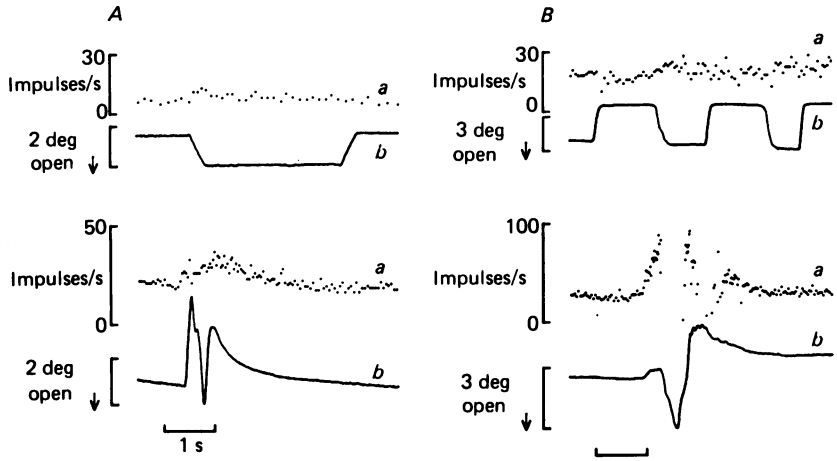

Fig. 3. *A*, tonic and *B*, modulated fusimotor activity during passive stretching (upper half of record), and during reflex movement of the jaw (lower half of the record). *a*, fusimotor; *b*, displacement. Neither fusimotor unit is affected by stretch. During active movements the tonic fusimotor smoothly increases firing without detailed relation to the movement, while the modulated fusimotor increases firing with closing, and is briefly silenced with opening.

These two varieties of fusimotor behaviour during reflex movements, as illustrated by the units in Fig. 3*A* and *B*, were called 'tonic' and 'modulated', respectively, as previously proposed by Appenteng *et al.* (1980). Thus, those units designated modulated displayed a striking modulation of activity with jaw closing, and reached firing rates of up to 100 impulses/s; in contrast, those units designated tonic appeared to match the envelope of the movement, rather than bearing any detailed relation to particular phases of the movement, and achieved more modest firing rates of up to 40 impulses/s. Of the thirteen fusimotor units identified in the present study, four were classified as tonic and nine as modulated. In several cases it was possible to record from a unit over several hours, during many reflex movements, and the pattern of activity was observed to be relatively stereotyped; that is to say a modulated unit never displayed tonic activity, nor a tonic unit modulated activity.

Simultaneous recordings of fusimotor and spindle activity during reflex movements. In order to correlate fusimotor and spindle activity patterns, simultaneous recordings were made from the cell bodies belonging to muscle spindle afferents of jaw-closing muscles in the mesencephalic nucleus of the fifth cranial nerve.

Previous studies have indicated that primary and secondary muscle spindle

afferents from jaw-closing muscles cannot be separated clearly on the basis of their dynamic response to stretch, their following of high frequency vibration, their inter-spike interval variability at constant muscle length (Cody *et al.* 1972) or the conduction velocity of their afferent fibres (Inoue *et al.* 1981). The latter study concluded that some 70% of spindle afferents in the masseter nerve fell into an intermediate, unclassifiable group using these criteria. However, both studies found that spindle afferents could be separated more reliably into primary and secondary afferent groups according to the effect of suxamethonium on the dynamic index of the unit.

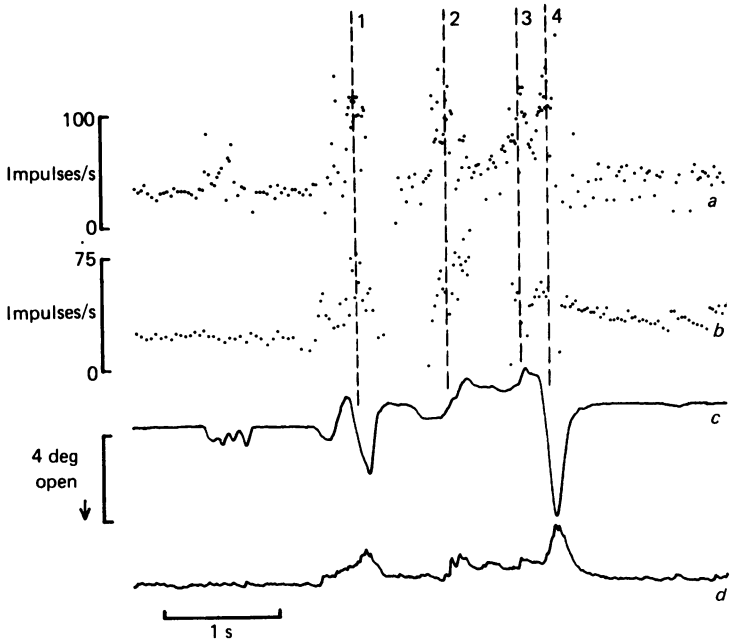

Fig. 4. Modulated fusimotor and secondary spindle afferent activity during reflex movements. *a*, secondary spindle afferent; *b*, modulated fusimotor; *c*, displacement; *d*, masseter e.m.g. 1 and 4, opening phases of movement; 2 and 3, closing phases. The afferent increases firing during shortening in parallel with the modulated fusimotor (see 2 and 3).

In the present study, eleven spindle afferents were recorded in the mesencephalic nucleus of the fifth nerve, and ten identified as primary or secondary on the basis of their dynamic index (Crowe & Matthews, 1964) during application of ramp stretches, before and after administration of suxamethonium. Before the administration of suxamethonium, the units fell into three groups according to their dynamic index: three units had low dynamic indices (less than 30 impulses/s), another three had high indices (greater than 90 impulses/s) and the remaining four had indices in an intermediate range (60–75 impulses/s). After administration of suxamethonium, the units fell into two groups, according to whether their dynamic index was increased or unaffected, and were identified, respectively, as primary or secondary. Simultaneous recordings were made from three pairs consisting of a secondary spindle afferent with a modulated fusimotor unit, five pairs consisting of

a primary spindle afferent with a tonic fusimotor unit and one pair consisting of a primary spindle afferent with a modulated fusimotor unit.

The simultaneously recorded activity of a modulated fusimotor and a secondary spindle afferent is illustrated in Fig. 4. As in the example of a modulated fusimotor in Fig. 3, the fusimotor firing frequency increases with jaw closing. The spindle is excited by the opening phases of the movement, labelled 1 and 4, to reach peak frequencies of 135 and 170 impulses/s respectively, as expected. However, it is also strongly excited during the closing phases labelled 2 and 3, reaching peak frequencies in a similar frequency range (140 and 120 impulses/s). At these times the muscle is actively shortening, yet failing to unload and silence the spindle afferent. Such an

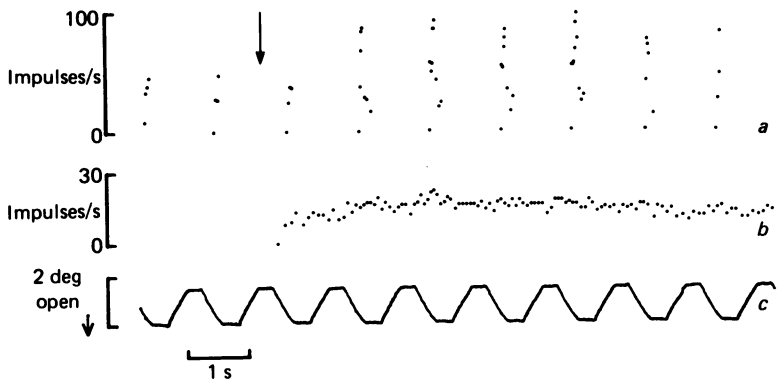

Fig. 5. Tonic fusimotor and primary spindle afferent activity during passive stretching of the jaw-closing muscles. *a*, primary spindle afferent; *b*, tonic fusimotor; *c*, displacement. Tail squeezing (indicated by arrow) recruits the fusimotor and is accompanied by an increase in the sensitivity of the primary afferent to stretch.

effect on a spindle secondary afferent could only be produced by static fusimotor activity during these phases, causing a sufficiently powerful intrafusal contraction to produce a net afferent excitation. The modulated fusimotor unit is, in fact, active during these two phases: in the closing movement labelled 2 it contributes a burst of activity, reaching a peak frequency of 90 impulses/s, and during the second, smaller closing movement labelled 3 it reaches a peak frequency of 55 impulses/s. During the first movement in the cycle, labelled 1, the fusimotor activity is slightly atypical in that it maintains a discharge throughout the movement, and lacks the more usual momentary pause in firing during opening (see Fig. 3). Note, however, that the firing of the secondary spindle afferent follows a rather similar pattern and also maintains its activity during the closing phases (as in 2 and 3 in Fig. 4). The closely parallel behaviour of the secondary spindle afferent and modulated fusimotor during closing (muscle shortening) suggests that the modulated unit may indeed be representative of a population of static fusimotor neurones.

Another feature of interest in this recording is the degree of independence of fusimotor activity from the masseter e.m.g. A small e.m.g. peak accompanies the closing movement labelled 2, as expected, and is accompanied by fusimotor activity. However, α-motor activity also occurs during the opening phases of the movement, as can be seen for example by the larger e.m.g. peaks in 1 and 4 in Fig. 4, and is

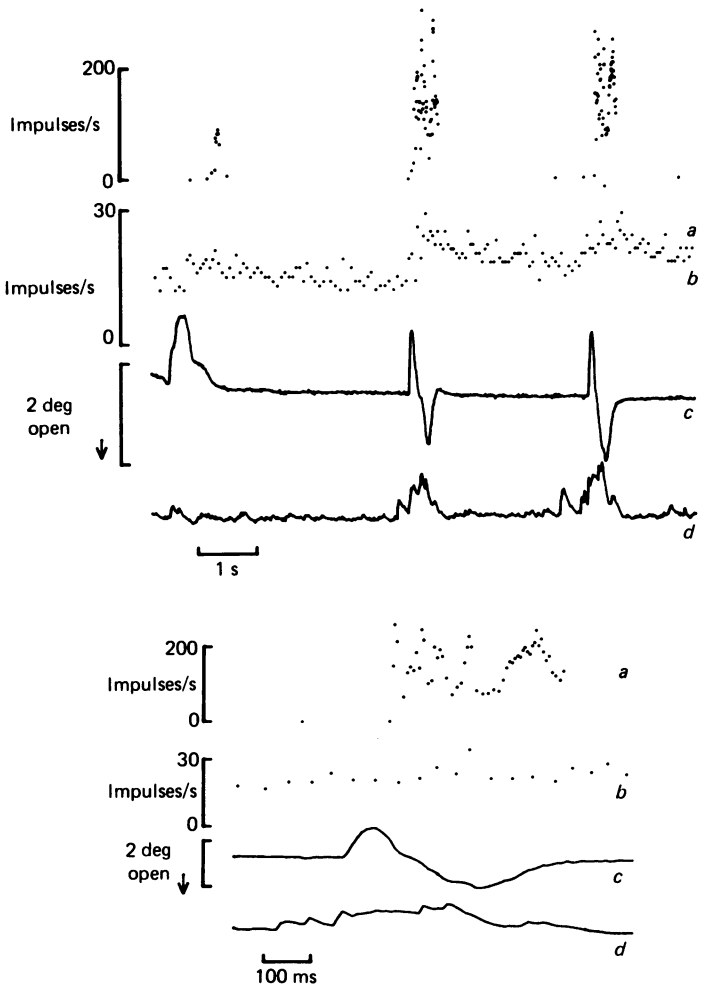

Fig. 6. Tonic fusimotor and primary spindle afferent activity during reflex movements (same unit as in Fig. 5). *a*, primary spindle afferent; *b*, tonic fusimotor; *c*, displacement; *d*, masseter e.m.g. (inset shows final movement in the series on an expanded time scale). The primary spindle afferent increases firing during lengthening and shortening of the jaw-closing muscles.

evidently stretch reflex activity. In this situation the α-motor activity is not accompanied by increased fusimotor discharge. Some potential independence of the two system is thus revealed. The final part of the movement sequence (4) is unlike the earlier parts in that it is not accompanied by a burst of fusimotion during closing. It is believed to be a swallowing movement in which, characteristically, jaw closing is achieved by relaxation of the opening muscles without active contraction of the closing muscles.

The activity of a tonic fusimotor and a primary spindle afferent is illustrated in Fig. 5, during continuous applied ramp stretches. The spindle is extremely phasic in behaviour. During the first part of the record, it has a modest dynamic response to

jaw opening, of about 46 impulses/s during which time the fusimotor unit is inactive. Squeezing the animal's tail then aroused the fusimotor to about 20 impulses/s, behaviour typical of a tonic fusimotor. This excitation is accompanied by an increase in the dynamic response of the afferent to 100 impulses/s, with no effect on discharge during the hold phase. This effect would appear to be dynamic in nature, strongly suggesting that the tonic fusimotor may indeed be representative of a population of dynamic fusimotor neurones.

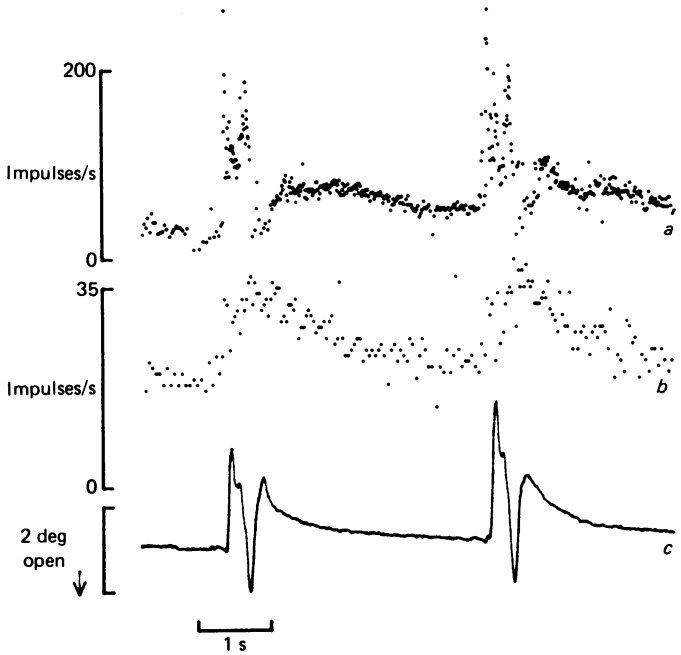

Fig. 7. Tonic fusimotor and primary spindle afferent activity during reflex movements (same fusimotor unit as in Figs. 5 and 6). *a*, primary spindle afferent; *b*, tonic fusimotor; *c*, displacement. The primary spindle afferent shows a similar discharge pattern to the afferent in Fig. 6, but maintains its discharge between movements.

The same pair of units is illustrated in Fig. 6, during a series of reflex movements. The fusimotor unit displays a pattern of activity similar to that illustrated in Fig. 3, smoothly increasing firing frequency during the movement to reach a peak frequency of about 30 impulses/s almost at the end of the movement. Although the afferent is capable of responding to stretch with a considerable degree of dynamic sensitivity, as seen in the previous record, it fails to respond to the rather irregular opening movement at the beginning of the record. However, later in the record both movements are accompanied by extremely high-frequency bursts of activity during the opening phases, to reach 300 impulses/s. As the tonic fusimotor has responded to both these movements, and not the first, it is likely that dynamic fusimotor fibres are discharging with a tonic pattern of the type seen here to cause the observed increase in dynamic sensitivity.

Closer examination of the record on an expanded time scale (Fig. 6, inset), reveals that the afferent is also active during the closing phases of the movement. It begins to fire as the movement commences, with closing, then reaches its maximum firing

rate during the opening phase, but continues to fire at a high frequency during the final closing phase. One might expect that such behaviour requires static fusimotor activity during the closing phase, as is indeed typical of the modulated type of behaviour.

A similar activity pattern was shown by the same fusimotor unit with a different primary afferent, during reflex movements, as illustrated in Fig. 7. The patterns of activity are generally similar to those displayed in Fig. 6, although the fusimotor reaches a slightly higher peak frequency of 36 impulses/s, and the movements are

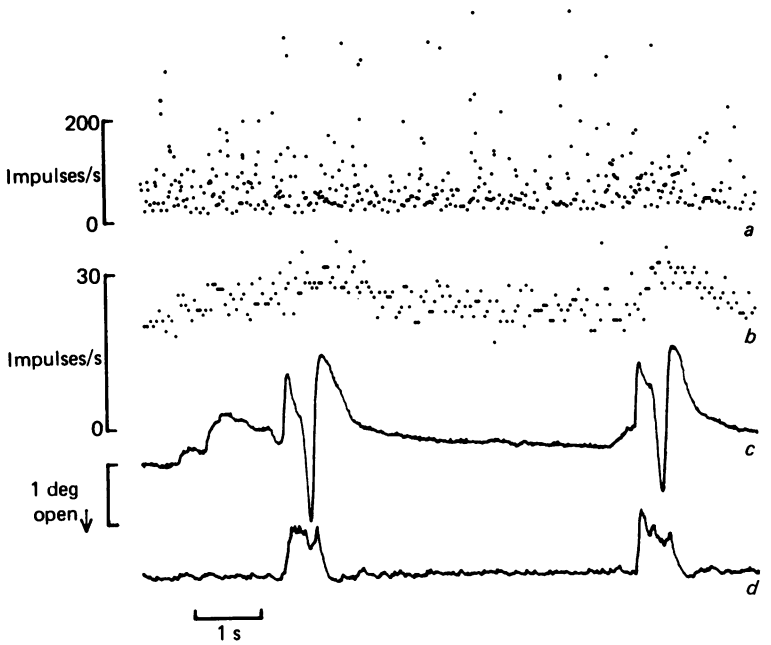

Fig. 8. Tonic fusimotor and primary spindle afferent activity during reflex movements. *a*, primary spindle afferent; *b*, tonic fusimotor; *c* displacement; *d*, masseter e.m.g. (same units as in Figs. 5 and 6). Primary afferent is now firing in an irregular manner, although the movements and fusimotor activity are similar to those in Fig. 6.

of larger amplitude. Once again, the primary afferent is excited during both opening and closing phases of the movement. However, a distinct feature of the behaviour of this primary afferent, in contrast to that shown in Fig. 6, is the appreciable maintained discharge during the slow increase in length at the end of the movement.

Clear evidence for a strong static fusimotor drive to a primary spindle afferent was found in one case, involving the tonic fusimotor and primary afferent illustrated in Fig. 6. In Fig. 6 the primary spindle afferent is extremely dynamically sensitive, and responds to both opening and closing phases of the reflex movement with a high-frequency burst of activity. A later recording of the same unit is illustrated in Fig. 8: note that the reflex movements are essentially similar to those in Fig. 6, and that they are accompanied by a comparable pattern of tonic fusimotor activity. However, the afferent now appears to have lost all dynamic sensitivity and is firing in an extremely irregular fashion. Such an effect on a primary afferent is classically

ascribed to the high-frequency activation of a nuclear chain fibre by a static fusimotor unit, and one must assume that such a fusimotor unit has been strongly excited. However, as the activity of the tonic fusimotor unit is unchanged, it is unlikely to be a candidate for an action of this sort.

DISCUSSION

Previous observations with this preparation which divided fusimotor fibres into tonic or modulated types (Appenteng *et al.* 1980) have been confirmed, and simultaneous recordings from spindle afferents have strengthened their identification as dynamic and static fusimotor fibres respectively. This identification rests on the observations that secondary spindle afferents can show peaks of discharge during muscle shortening similar in time course to the firing of the modulated unit, whereas recruitment of tonic units (by cutaneous arousal stimuli) is associated with an enhancement of the dynamic sensitivity of primary spindle afferents to passive stretch.

Given that this interpretation is correct, the findings of this paper add support to the previous proposal that during reflex jaw movements the dynamic fusimotor neurones of the jaw-closing muscles increase their firing in a tonic fashion, without any detailed correlation with the α-motor activity or with the movement (Appenteng *et al.* 1980; Taylor, Appenteng & Morimoto, 1981). It is true that this evidence comes from the anaesthetized animal in which motor control is clearly very disordered. However, it agrees generally with results from recordings of jaw muscle spindle afferents in fully conscious and active cats (Cody *et al.* 1975). In these experiments it was noted that the dynamic sensitivity of spindle primaries was generally higher during active movements than in identical passive movements under deep anaesthesia and that there was often very great sensitivity to small, slow muscle lengthening during active movements. Similar findings were reported for cat hind-limb muscles by Prochazka *et al.* (1977). In none of this work would it be appropriate to describe dynamic fusimotor behaviour as showing α–γ co-activation. It seems better to regard the build-up of dynamic fusimotor activity during movement as providing the correct background sensitivity of the muscle spindle primary afferents to dynamic length changes.

As Matthews (1972) points out, the dynamic fusimotor fibres do not cause a sufficiently rapid intrafusal contraction to enable them to keep primary afferents firing during any but the slowest rates of shortening. It would therefore be inappropriate for them to be modulated rapidly during fast cyclic movements in parallel with the α-motoneurones. Recent studies of γ-motoneurone reflexes (Appelberg, Hulliger, Johansson & Sojka, 1983) also emphasize the relatively greater independence of dynamic fusimotor than static fusimotor neurones from α-motoneurones.

The present work supports the belief that static fusimotor fibres, in contrast, can show rapidly and strongly modulated discharge during active movements, roughly in parallel with the muscle shortening. Again the results might be criticized as not necessarily representing normal behaviour because of the anaesthesia, but they do agree well with interpretation of spindle recordings in conscious animals. In such experiments (Cody *et al.* 1975) it was concluded that static fusimotor firing could be

low or absent during muscle lengthening, but be enhanced during shortening. The effects of static fusimotor firing modulated in this way during muscle length changes are not precisely known, but it is clear that intrafusal contractions induced by static fusimotor stimulation are much more rapid than those due to dynamic action (Bessou, Laporte & Pagés, 1968). Thus it would make functional sense for static fusimotor firing to be modulated rapidly during muscle contraction in such a way as to tend to prevent unloading of the primary and secondary afferents. In support of this, Lennerstrand & Thoden (1968*a*, *b*) showed that static fusimotor stimulation was more effective than dynamic at supporting primary afferent firing during muscle shortening. It has also been shown (Hulliger, 1979) that static fusimotor stimulation is on average some 4·7 times more powerful than dynamic in producing changes in firing frequency of primary afferents. Recently, Appenteng, Prochazka, Proske & Wand (1982) have specifically tested the possibility of modulating fusimotor firing to keep primary afferent discharge constant during muscle shortening. They showed that continued stimulation of a number of fusimotor filaments could indeed achieve this in all except the very fastest physiologically occurring rates of shortening. Though the relative roles of static and dynamic fusimotor fibres could not be separated with certainty, the results were certainly not inconsistent with the greater importance in this respect being accorded to the static system.

The extent to which fusimotor firing can compensate for shortening in natural conditions was revealed by further recent recordings from jaw muscle spindles in fully conscious cats (Taylor & Appenteng, 1981). During mastication of soft food a spindle primary could follow larger, fast movements in both lengthening and shortening such that the spindle looked like a length receptor with a large, generally linear, dynamic range of action. It clearly received some extra fusimotor drive (presumably static) during shortening; otherwise it would certainly have become silent. When tougher food was encountered, as indicated by slower shortening despite increased e.m.g. activity, the spindle firing actually *increased* considerably during the shortening phase, at a time when we would expect from the present work to observe a burst of static fusimotor firing. The attribution of this type of effect to static discharge was strengthened by recordings from a secondary afferent during lapping. In this case also, rather simple length transduction characterized the unit under normal conditions, but when a small I.V. dose of anaesthetic was given lapping movements continued more slowly and at about half the normal amplitude. Firing during lengthening continued as before, but now there was firing during *shortening* in addition, with a temporal pattern similar to that of our modulated fusimotor fibres. The existence of this drive was revealed because of the reduction of speed and extent of the active shortening. It seems that light anaesthesia depresses α-motor more than fusimotor activity.

It may be tempting to argue that the presently observed strong modulation of static fusimotor firing roughly in parallel with α firing could be described as α–γ co-activation. We would argue against this however, in that the parallelism between α- and γ-motoneurone firing is not at all constant and the term 'co-activation' though not usually clearly defined, implies a rather rigid linkage between the two systems. It has been shown repeatedly that there is in fact considerable opportunity for independence of action (see especially Matthews, 1972 (chapter 9); 1981).

In the original proposal for the 'length follow-up servo' (Merton, 1953) control of

contraction it was thought that, for some movements, the command would be predominantly via the γ system (now best interpreted as γ_s). There is no evidence from *natural* movements that the fusimotor drive is ever strong enough to generate the movements via the 'γ loop' in this way. The later modification of this scheme to a principle of 'servo-assistance' (Matthews, 1972, 1981) is compatible with the present data since if the γ_s discharge is enhanced during shortening enough to keep the spindle afferents firing (as is often the case), then it is undeniable that the γ_s signal is providing part of the drive to contract the muscle via the reflex loop, and conditions would be favourable for feed-back correction of disturbances due to mechanical loading. However, the usual net result of the patterned static fusimotor drive and the direct α drive would be that the spindles behave as displacement sensors with a wide dynamic range. Departure from smooth reduction or silencing of firing during shortening would only occur if there were unexpected loading or if α-motor firing were relatively reduced. For these reasons we think there may be an advantage in regarding the modulated pattern of static fusimotor discharge as a 'temporal template' of the intended movement (see Taylor *et al.* 1981; Taylor & Appenteng, 1981). Phillips (1969) favoured the idea of a fusimotor discharge varying in parallel with muscle length, but thought that this might result in constant firing frequency when the movement proceeded according to plan. We have occasionally observed periods of relatively constant firing of primary spindle afferents during large movements (Cody *et al.* 1975, and above), but it seems that this may occur through the action of strong constant drive to the nuclear chain fibres (Boyd, Gladden & Ward, 1983) and may be a sign of the occasional use of a quite different strategy. Boyd has made it increasingly clear that the interpretation of fusimotor effects should be based on the type of intrafusal muscle fibre activated: bag_1, bag_2 or chain, rather than in terms of γ_d and γ_s nerve fibres. This leaves open the question of whether there may be some degree of separate control available over the bag_2 and the chain fibres.

Thus the interpretation offered for fusimotor action in reflex jaw movements is that the dynamic system provides 'parameter' control as visualized by Matthews (1981), while the static system generally provides a pattern of the intended movement, described as a 'temporal template'. This would mean that the static firing profile would generally resemble that of α activity, but the very different reflex connectivity of the two systems will cause frequent departures from a firm α–γ co-activation (see also Appelberg *et al.* 1983). This scheme does not reject the idea that 'servo-assistance' is in operation, though it has usually been taken that this requires the net spindle afferent firing to be kept constant. It may rather be argued that as long as the movement proceeds in reasonable match to the 'temporal template' of the static fusimotor discharge then some afferent activity will continue throughout active muscle shortening and the benefits of negative feed-back will be exploited.

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