Fusimotor influence on jaw muscle spindle activity during swallowing-related movements in the cat

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1. The activity patterns of muscle spindle afferents in jaw-closer muscles were studied during reflex swallowing movements in anaesthetized cats. Simultaneous records were made of the electromyogram (EMG) in masseter and anterior digastric muscles and of the unloaded jaw movements. The underlying patterns of fusimotor activity were deduced by comparing afferent discharges occurring during active swallowing with those occurring when exactly the same movements were imposed passively. The interpretation of spindle behaviour was greatly facilitated by characterizing the afferents according to the evidence for their contact with the various intrafusal muscle fibres, derived from testing with succinylcholine. It was also valuable to have two different types of afferent recorded simultaneously.

2. There was clear evidence of fusimotor activity occurring during active jaw closing so as to oppose the spindle silencing. This effect was most marked in b_2c-type afferents (probably secondaries) and was therefore attributed to a modulation of static fusimotor discharge approximately in parallel with α-activity.

3. Afferents with evidence of bag_1 fibre contacts (primaries) showed much greater sensitivity to muscle lengthening during active movement than when the movement was imposed. This difference was exaggerated when anaesthesia was deepened for the passive movements. This was interpreted as evidence for a higher level of dynamic fusimotor activity maintained during active movements than at rest.

4. The results support the view that for a variety of active jaw movements, static fusimotor neurone firing is modulated roughly in parallel with α-activity but leading it so as to counteract spindle unloading. Dynamic fusimotor neurone firing appears to be set at a raised level during active movements. Anaesthesia appears to depress activity in the α-motoneurones more than in γ-motoneurones.

The potential advantages of feedback control of voluntary movements by means of muscle spindles are well recognized (Merton, 1953; Matthews, 1972, 1981; Prochazka & Hulliger, 1983). However, a clear appreciation of the actual role of muscle spindles in any given type of movement has always been hampered because of uncertainties regarding the patterns of activity occurring in the γ-motor supply, which can dramatically alter the response of primary and secondary spindle afferents to muscle length changes. The basic experimental problem is the difficulty of recording the activity of γ-motoneurones directly during natural movements and of identifying them as static or dynamic. The alternative approach is to record spindle afferent activity and to use this combined with the movement record to deduce the underlying fusimotor firing patterns. Previous observations of this kind on cat jaw-closing muscles (Cody & Taylor, 1973; Taylor & Cody, 1974; Taylor & Appenteng, 1981) have led to the conclusion that during lapping and eating the usual pattern is for dynamic fusimotor activity to be tonically increased during a movement sequence and for static fusimotor firing to be modulated approximately in parallel with α-motor activity.

Related observations in other situations have led to rather different views. Thus, in alert locomoting cats, Prochazka, Hulliger, Trend & Durmuller (1987) could explain the recorded spindle afferent firing on the basis of purely tonic levels of static and dynamic firing with no modulation. On the other hand, from observations in the high decerebrate locomoting cat it was deduced that static fusimotor firing was maintained at a tonic level while dynamic discharge was strongly modulated (Murphy, Stein & Taylor, 1984). Human microneurography has indicated changes in fusimotor activity during limb movements, but these changes have not been specified as static or dynamic (Vallbo, 1985; Ribot, Roll & Vedel, 1986).

Clearly, there is a need for more data to be gathered on spindle behaviour in a variety of conditions and this paper presents results from some new experiments on jaw-closing muscle spindles in the lightly anaesthetized cat. This

preparation is convenient because the animal will make repeatable jaw movement patterns in response to placing water in the mouth and the firing of single spindle afferents can be recorded, with very little trauma, from the cells of the mesencephalic trigeminal nucleus (MeV). The present experiments improve on previous similar ones in that new ways of interpreting the effects of succinylcholine (SCh) on spindles (Taylor, Durbaba & Rodgers, 1992*a*) now permit confident deductions to be made as to the contacts which each afferent makes on bag_1, bag_2 and chain intrafusal muscle fibres and hence the interpretation in terms of static and dynamic fusimotor action. Also, we now compare spindle firing during active movements with firing of the same units whilst the same movements are reproduced passively. This has been attempted before (Taylor & Davey, 1968; Loeb & Hoffer, 1985), but is now combined with computer averaging and subtraction so as to give much clearer conclusions regarding the underlying fusimotor patterns occurring naturally in these movements.

METHODS

Eight cats were used in the weight range 3·2–5·2 kg. Anaesthesia was induced by 2% halothane in oxygen administered in a box and continued via a mask during insertion of a tracheal cannula and subsequently through this. After insertion of two venous cannulae, one in the cephalic vein of each forelimb (one for anaesthetic and one for SCh) and a cannula in the right femoral artery for monitoring blood pressure, halothane was discontinued and α-chloralose (40 mg kg^{-1}) administered I.V. Mean arterial blood pressure remained stable in the range 85–100 mmHg for 3–4 h, after which anaesthesia was supplemented by I.V. doses of ketamine (1 mg kg^{-1}), thiopentone (25 mg kg^{-1}) or further doses of chloralose (15 mg kg^{-1}) as necessary, if the blood pressure rose more than 10 mmHg above its original stable level. Additional anaesthetic was also routinely given before testing with SCh.

A screw bearing a stainless-steel rod (15 needle gauge, 15 mm length) was inserted into a hole drilled into the symphysis menti. This was for the attachment of a miniature lamp needed for the photoelectric movement recording system and for connection to an electromagnetic servo system for moving the jaw passively. In later experiments the attachment of the servo to the jaw was made through a light clamp with screw points inserted into small holes drilled in the lateral surface of the mandible adjacent to the second premolar teeth. Pairs of enamelled silver wires were inserted into anterior digastric, masseter and sometimes anterior temporalis muscles on the left side for EMG recording. The animal was then transferred to a stereotaxic frame and the back supported by a clamp on the first lumbar vertebra. All pressure points and sites of skin incisions were first infiltrated with 1% lidocaine (lignocaine). A craniotomy was made to allow access to the MeV on both sides, the dura reflected and a small pool formed with 1·5% agar to be filled with liquid paraffin. Two electrodes were used to record from two different spindle afferents, one mounted vertically, the other angled backward and downward at an angle of 10 deg to the vertical in a parasagittal plane 2·3 mm lateral to the mid-line. They were displaced between 1 and 2 mm rostral to the earbar zero to reach the more rostral part of the MeV (approximately 16·5 mm below the cortical surface), where the spindle afferent cells are generally well dispersed, to permit isolation of single units. For background information on recording from jaw muscle spindles see Taylor (1990).

Electrodes were of glass-coated tungsten with the 20 μm exposed tip plated with platinum black (A. Ainsworth, Walthamstow, Essex, UK). Each was advanced with a stepping motor drive while the jaw was moved sinusoidally with 2·5 deg amplitude at 1 Hz. It was usually possible to isolate two separate spindle afferents in this way and to retain stable recording for an hour or more. Identification of the muscle of origin was usually possible by light surface probing (Cody, Lee & Taylor, 1972; Taylor *et al.* 1992*a*).

Jaw movement in the vertical plane was recorded without loading by a device based on a Schottky PIN photo-diode (Quantrad Corporation PS-200-4, Los Angeles, CA, USA) similar to that described by Luschei & Goodwin (1974). During active movements the jaw was freed from the electromagnetic servo and the photo-transducer output was recorded on magnetic tape (TEAC RD120T). Subsequently, on replay the magnetic tape output was connected to the servo, which was re-attached to the jaw. Adjustments were made to ensure that on replay the starting position and the amplitude of the movements were exactly the same as during recording.

Unitary spikes were discriminated and recorded as events using the Spike2 program running on a 486 66 MHz PC with the CED 1401plus interface (Cambridge Electronic Design Ltd, Cambridge, UK). Jaw movement records were sampled at 200 Hz. The EMG signals were filtered from 50 Hz to 1 kHz, sampled at 2 kHz and logged with the same system. Records were first processed with Spike2 and then the data transferred to a Macintosh Centris computer for further processing using Kaleidagraph (Synergy Software Inc., Reading, PA, USA).

After recordings had been made of active and passive movements, spindle afferents were tested with SCh in a way similar to that previously described (Taylor *et al.* 1992*a*). Ramp and hold stretches were applied to the lower jaw continuously, repeating every 6 s. The stretch was of 10 deg amplitude. It was maintained for 1·5 s and the velocity of lengthening and shortening was 10 deg s^{-1}. The test was preceded by administration of 2 mg ketamine I.V. to reduce on-going γ-motor activity. After five control stretches SCh (200 μg kg^{-1} in 1 ml saline) was injected I.V. and the recording continued for 5 min. The interpretation of the responses has been dealt with in detail previously (Taylor *et al.* 1992*a*; Taylor, Rodgers, Fowle & Durbaba, 1992*b*), but briefly the strength of influence on an afferent by bag_1 intrafusal fibres is estimated by the increase in the response to dynamic stretch caused by SCh. The influence of bag_2 fibres is estimated by the increase caused by SCh in initial frequency (i.e. the mean frequency in the 0·5 s immediately before each stretch in the cyclically repeating stretches as described). In this way each spindle afferent could be characterized according to the influence upon it of the intrafusal muscle fibres as b_1c, b_1b_2c, b_2c or c type. A period of at least 30 min was allowed for recovery from SCh before making further recordings.

At the end of the experiments the animals were killed by an overdose of sodium pentobarbitone administered intravenously.

RESULTS

Useful data were obtained from seven cats. Swallowing movements could generally be elicited reliably for some 2–4 h after the preparation was set up. Subsequently, the animal tended to become unresponsive, although its condition

remained good as indicated by steady blood pressure and respiratory movements. Because of this and the time taken to isolate and fully test the spindle units, the number which could be examined in each experiment was limited. Altogether thirty-nine afferents were examined, nineteen in temporalis, four in masseter and sixteen in which the jaw-closing muscle of origin could not be determined. Of the total, twenty-seven were recorded in active and passive movements and these provide the basis for the present report. Testing with SCh was carried out in twenty-four units and they were identified as the following types: b_1c (2), b_1b_2c (11), b_2c (7) and c (4).

Examples of responses during swallowing are shown in Fig. 1*A*. Each active movement was induced by squirting about 5 ml of water through a plastic cannula over the posterior dorsum of the tongue into the pharynx. The initial closing movement started slowly and then became rapid. It was followed by opening and finally a slower return to the starting position. Masseter EMG activity was seen to increase to a maximum at the peak of the closing movement, then to return to zero during the ensuing opening movement. The final return to the starting position was slower and was a passive process without masseter activity. Digastric EMG showed activity extending throughout the swallowing movement. There was a marked burst during the initial closing and a second phase of activity during opening. Behaviour of this kind in anterior digastric has been reported previously (Thexton & McGarrick, 1994). Evidently, during swallowing digastric is not simply an antagonist of masseter, but is probably contributing to elevation of the floor of the mouth during the initial closing.

The spindle afferent discharge from the jaw-closer is very irregular (Fig. 1*D*). Firing is generally at a low frequency between the movements, but increases from the beginning of jaw closing, that is the muscle *shortening*, and reaches a maximum during opening. When the same movements were

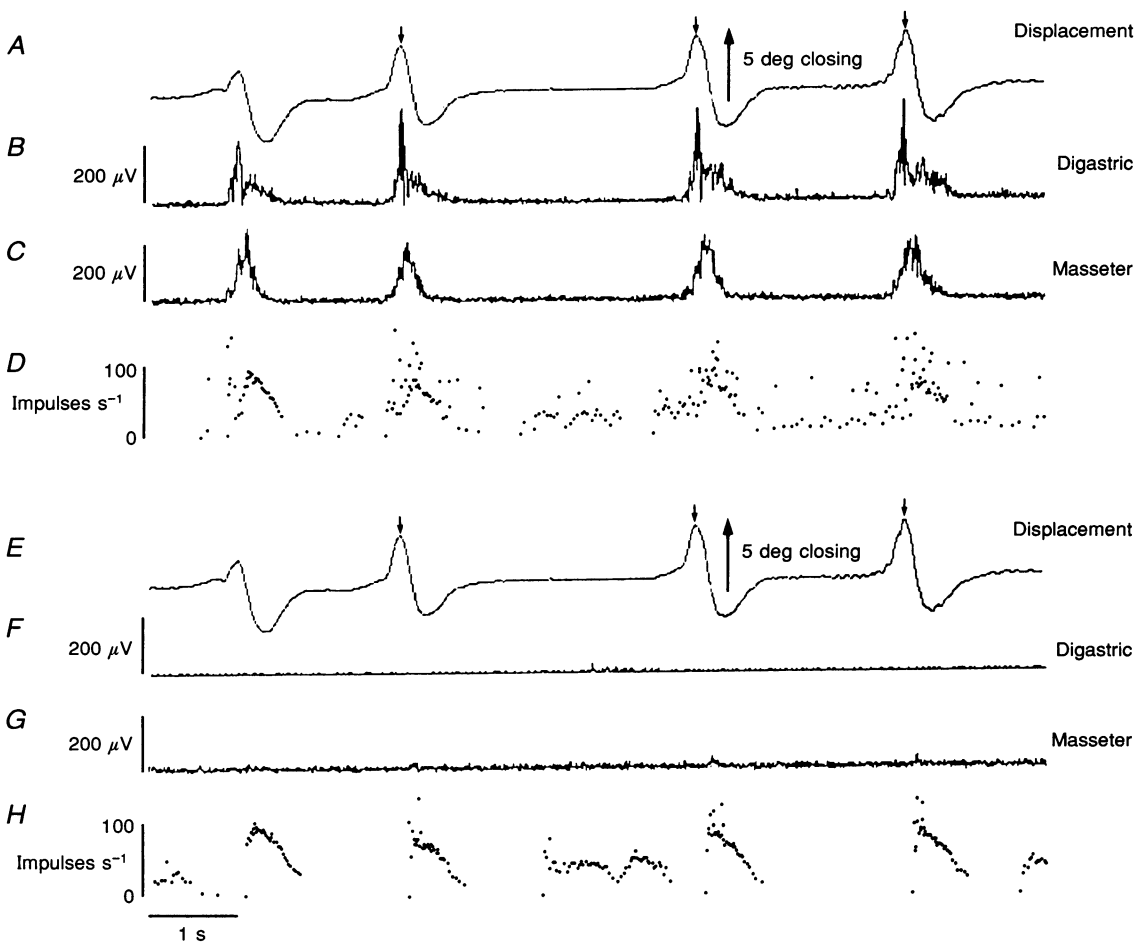

Figure 1. Jaw-closer muscle spindle afferent firing in active and passive movements

A, unloaded jaw movements in response to placing fluid in the mouth. The first movement is identified as belonging to a different pattern from the other three. *B* and *C*, smoothed rectified digastric and masseter EMG. *D*, spindle afferent instantaneous frequency during active movements. During the passively replayed movements (*E*) the digastric and masseter EMG records are silent (*F* and *G*) while the spindle (*H*) shows less irregularity and is silenced during the muscle shortening phases. Small arrows on the displacement records indicate the time zero marks for averaging three of the movement cycles as in Fig. 2.

reproduced passively, the spindle firing was more regular, dropped to zero during jaw closing and rapidly reached a peak during the subsequent opening (Fig. 1*H*). There were thus very clear differences between active and passive behaviour, indicating differences in fusimotor activity between the two states.

In order to estimate how fusimotor activity varied, spindle discharge occurring during passive movements was to be subtracted from that during active movements. Because of the irregularity of spindle discharge, this was best carried out on records averaged across a number of closely similar movements. The relative size and speed of the components of a movement sequence could vary, but on reviewing the records on the computer screen it was possible to identify two or three distinctly different patterns and place time markers on a clearly defined feature of each, usually the peak of the closing movement. By aligning a number of movements (5–15) of similar pattern by means of these time marks, average time courses could be computed of spindle discharge, jaw movement and rectified EMG. Finally, averaged spindle discharge recorded during passive movements could be subtracted from that recorded during active movements of exactly the same form. Afferent spikes were averaged in 25 ms bins, which were finally subjected to three-point smoothing with equal weighting. This provides a low-pass filter function with no phase shift at frequencies less than 13·3 Hz. Figure 2 shows the process applied to six movements of similar pattern of which three are marked with arrows in Fig. 1. The averaged spindle discharge during active movements (■) diverges from that seen for the imposed movements (▲) at the onset of the jaw closing. The difference between the two states shows very clearly as a marked increase in firing starting immediately before and increasing during the active muscle shortening period. The difference frequency (Fig. 2*B*), which in this case reaches a maximum of 60 impulses s^{-1}, can be seen in Fig. 2*A* to be composed of some 20 impulses s^{-1} due to unloading in the passive state together with 40 impulses s^{-1} increase in frequency occurring during active shortening. Such an effect can reasonably be attributed to a burst of static fusimotor firing starting just before and continuing throughout active shortening. The difference falls to close to zero during the muscle lengthening period. This implies that the burst of fusimotor activity does not continue beyond the jaw-closing phase.

Figure 3*A* and *B* shows averaged afferent firing differences for two movement patterns selected from the same record and superimposed on the active movement records. Within the continuous recording of about twenty swallows, two distinct movement patterns could be recognized. They were marked and selected into two groups for averaging separately. It is clear that despite the variation in the

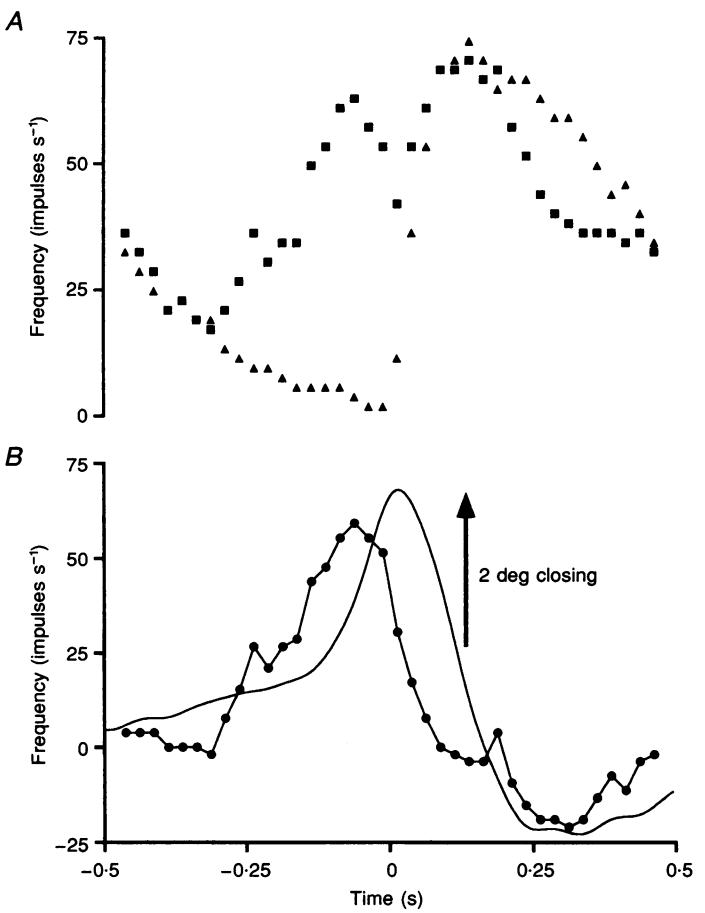

Figure 2. Spindle responses averaged over repeated similar swallowing movements

A, spindle averaged firing frequency in 6 active (■) and passive (▲) movements. *B*, the averaged active movement pattern is shown by the continuous smooth line. The difference between the frequency records (active − passive) is shown by ●. Spindle unit is the same as in Fig. 1.

movement pattern, the general form of the difference caused by fusimotor activity remains essentially similar. This figure also shows the mean masseter EMG profiles taken from the active movements. The onset of the fusimotor effect, as estimated by the afferent firing difference plot, leads the EMG activity by between 100 and 200 ms. It also appears that the fusimotor activity ends before the α-motor activity.

The dynamic sensitivity of this afferent to muscle stretch does not appear to be different in the active and passive states. Since testing with SCh was not possible for this particular unit, it cannot be decided whether the constancy of dynamic sensitivity was because the afferent made no contacts with a bag_1 fibre or alternatively because there was no change in dynamic fusimotor activity. A favourable situation for testing this issue is shown in Fig. 4 in which results from two spindle afferents recorded simultaneously are shown. Testing with SCh showed that the upper unit was of b_2c type while the lower one was of b_1c type. There is a clear contrast between the two in the rapid jaw-opening phase. The lower unit shows a peak in the difference between active and passive movement conditions, which means that the firing caused by muscle stretch during the active movement was much greater than that during the passive movement. This implies the presence of enhanced dynamic fusimotor firing during active movements, which can show itself in the behaviour of this unit because, as the SCh test revealed, it is influenced by bag_1 fibre contraction. On the other hand, the upper unit, which has no influence from a bag_1 fibre, shows a falling difference frequency during the muscle lengthening phase. This could be explained by a falling static fusimotor firing at this time during the active condition.

The importance of dynamic fusimotor activity in the active condition is emphasized by the behaviour of a b_1b_2c-type afferent as seen in Fig. 5. In this case, after recording active and passive movements in the usual way a further dose of anaesthetic was given and the passive movement repeated. The records show that the active–passive difference during the jaw-opening phase is greater when the passive movement was made after deepening the level of anaesthesia (▲) than before (■). This is most easily interpreted as due to a level of dynamic fusimotor activity which is high during active movements, lower in the passive state directly afterwards and lower still in deep anaesthesia. It is not possible to say from this evidence whether the enhanced dynamic activity is maintained tonically throughout the movement sequences, but as will be discussed later, other observations support this view. A plot of the time course of the difference between light and deep anaesthesia is shown in Fig. 5*B*. It is clear that the difference is entirely restricted to the muscle lengthening phase. This is to be expected if the difference is due to a higher level of tonic dynamic fusimotor activity in the lightly anaesthetized state, because dynamic activity enhances the response of the spindle primary ending to

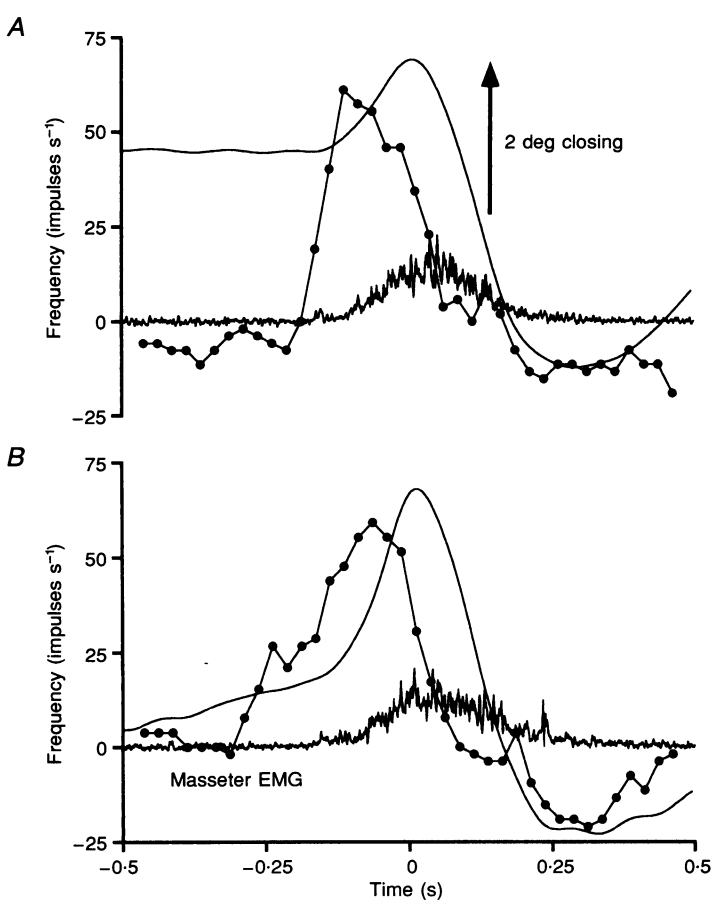

Figure 3. Responses averaged for two different movement profiles

The movement records (continuous smooth lines) in *B* show a slower initial closing phase followed by a larger fast closing phase than those in *A*. The differences in spindle firing frequency (●) were obtained by subtracting the mean records for the passive movements from those for the active movements. Masseter EMG records are from the active movements and were rectified and smoothed before averaging. The number of movements averaged was 7 for *A* and 6 for *B*. All were taken from one continuous recording.

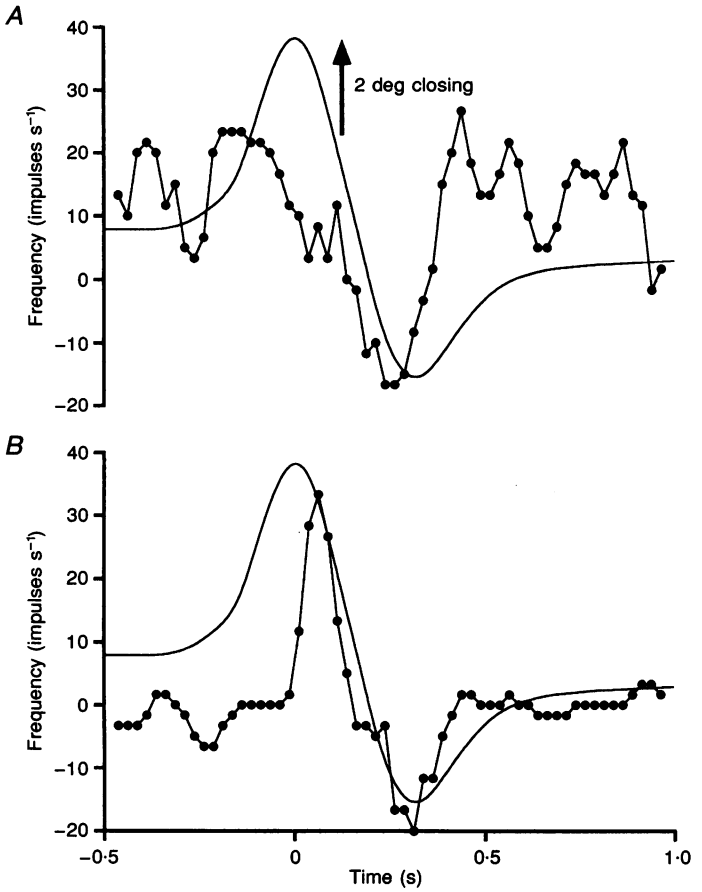

Figure 4. Simultaneous recordings from two jaw-closer spindle afferents

Continuous smooth lines are the averaged active movements, lines with ● are the averaged differences in firing (active − passive). The unit in *A* was identified by SCh testing as b_2c and that in *B* as b_1c. The number of movements averaged was 8.

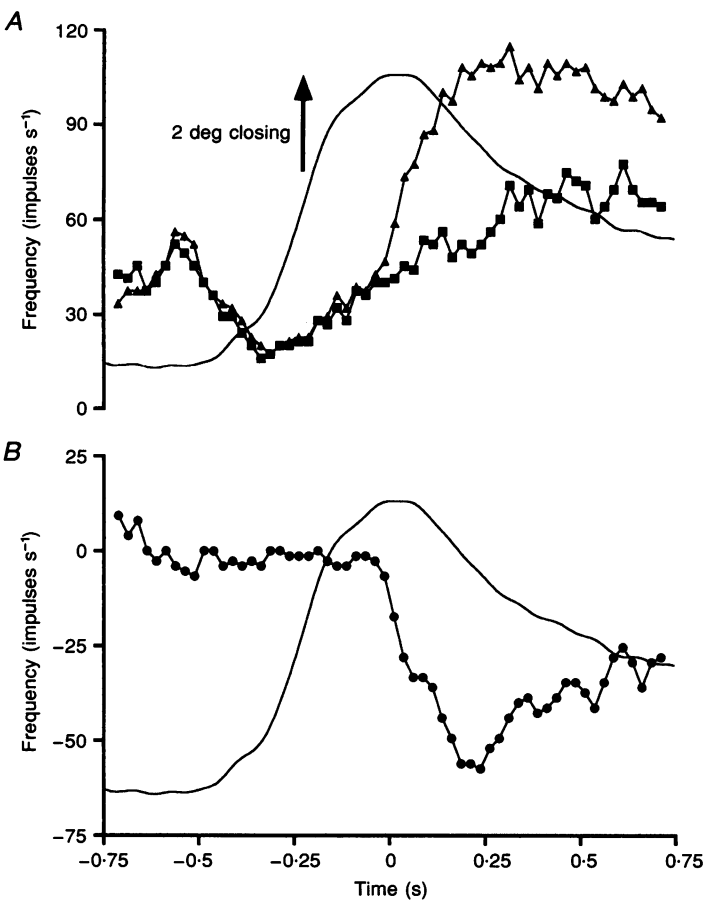

Figure 5. Effect of increasing depth of anaesthesia on the response of a b_1b_2c unit

A, active movement pattern averaged from 10 records (continuous smooth line) and the difference in the spindle discharge between active and passive movements. In one case (■) the passive movements were made under light anaesthesia; in the other (▲) the level of anaesthesia was deepened for the passive movements. *B*, averaged movement pattern and the difference between the two difference plots in *A* (i.e. light − deep anaesthesia).

stretch but has little effect on the response during shortening (Crowe & Matthews, 1964; Lennerstrand & Thoden, 1968). The response during shortening is dominated by static fusimotor activity (see p. 211 of Matthews, 1972).

It was a regular finding that spindle afferents showing evidence from their responses to SCh of bag_1 fibre influence (primary afferents) had a much higher frequency of discharge during jaw opening in the active state than in the passive movement. On the other hand, those without bag_1 fibre influence (secondary or b_2c primary – see Taylor *et al.* 1992*a*) responded to passive opening much more than to active opening. This is well illustrated in Fig. 6 in which average movement and frequency difference plots have been averaged for four b_2c units (Fig. 6*A*) and for four b_1b_2c units (Fig. 6*B*). The similarity of the mean movement waveforms in the two cases confirms the repeatability of the swallowing pattern across different experiments and so supports the validity of constructing such average plots. The average frequency difference curves show very clearly the peak during muscle shortening for the b_2c units and the peak during lengthening for the b_1b_2c units. In the nine out of eleven recordings of b_2c- or c-type afferent units for which repeatable active movements were recorded, all showed greater discharge in active compared with passive shortening. In the eleven out of thirteen b_1b_2c or b_1c units in which active and passive movements could be compared, all showed an excess of discharge during active lengthening. Five out of eleven also showed some increase of active over passive firing in the shortening phase. The unit responses averaged in Fig. 6*A* and *B* were chosen because the active movement patterns available were sufficiently similar to warrant averaging across units. We can thus regard it as a reliable observation that the fusimotor pattern underlying swallowing movements is such as to oppose unloading during active muscle shortening. This effect, being most clearly seen in b_2c units, must be due to static fusimotor activity. It is also clear that since much greater dynamic sensitivity to stretch is seen in active movements than in passive and that this effect is seen only in units with b_1 intrafusal fibre influence (primary afferents), then dynamic fusimotor activity must be increased during active movements.

Another way of revealing fusimotor changes accompanying a movement is to follow the spindle firing while the movement is arrested as in Fig. 7. Averaged unloaded jaw movements and masseter and digastric EMG are shown in Fig. 7*A*. Directly after this recording the mandible clamp was fixed and another set of swallowing responses recorded to yield the averages in Fig. 7*B*. Here the records have been aligned using the onset of digastric EMG. It can be seen that the amplitude of the averaged EMG record in Fig. 7*B* is greater than in Fig. 7*A*. This is consistent with the operation of some degree of load compensation. Figure 7*C* shows the averaged frequencies of two spindle afferents unloaded as in Fig. 7*A*. The b_2c unit (●) shows little frequency fluctuation, while the b_1b_2c unit (▲) shows a

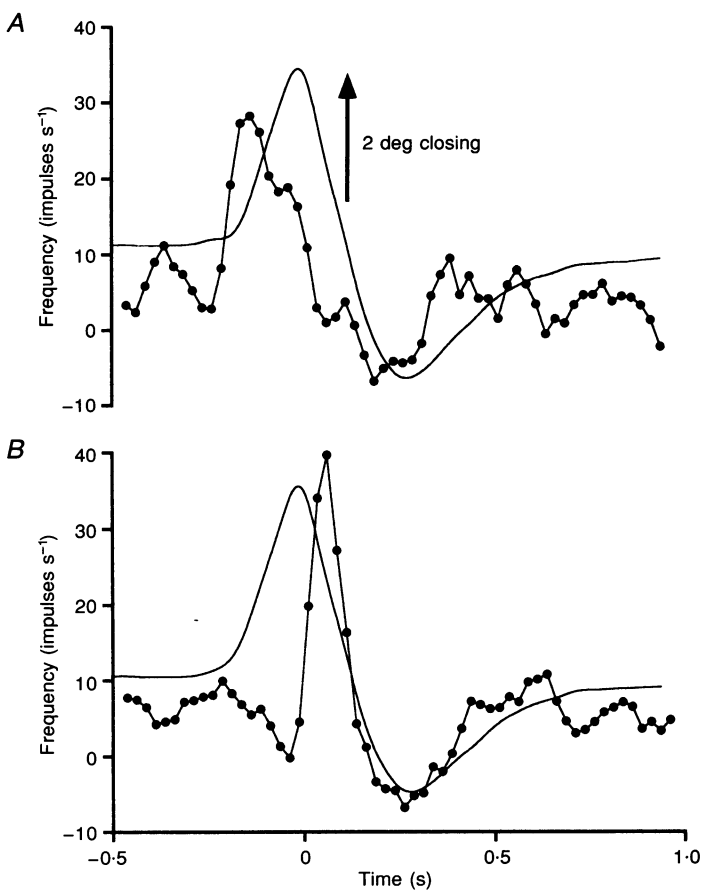

Figure 6. Mean response of b_2c- and b_1b_2c-type units

A and *B* are, respectively, the averages of mean responses from 4 units each of b_2c and b_1b_2c type. In each case the continuous smooth line is the averaged movement pattern and ● indicates the mean frequency differences (active − passive).

marked burst during muscle lengthening. The result of applying the same movements passively is seen in Fig. 7*D* and the difference plots in Fig. 7*E*. As in the previous comparison of two such units, the b_2c afferent showed a positive difference during the jaw-closing movement, whereas the b_1b_2c did not. In Fig. 7*F* the movements were obstructed as in Fig. 7*B* and now it is evident from its firing frequency increase that the b_2c unit is being excited by a burst of static fusimotor activity starting just before the onset of the masseter EMG. This effect is very much weaker in the b_1b_2c unit. It seems likely that the greater dynamic sensitivity of the latter type of afferent makes it more difficult for the static fusimotor burst to prevent unloading than is the case for the b_2c type. Another difference in the records of the two units in Fig. 7*F* is that the b_1b_2c unit appears to silence during the onset of the masseter contraction and to fire again during the offset of the contraction. This behaviour is probably because the contraction causes some internal shortening of the muscle, which unloads the afferent because it is very dynamically sensitive. The effect of obstructing the movement was recorded satisfactorily for two additional afferents which were identified as b_2c type. Both showed behaviour similar to that seen in Fig. 7, one increasing its frequency by 50 impulses s^{-1} during the masseter contraction phase.

DISCUSSION

The present findings support the view that static fusimotor firing is strongly modulated during the course of jaw movements. The evidence is based upon the comparison of spindle discharge during active and exactly matched passive movements and shows that the increased static fusimotor firing approximately parallels and slightly leads the extrafusal muscle contraction. In the lightly anaesthetized cat this fusimotor firing is sufficient often to cause a nett increase in firing frequency of spindle afferents, which would otherwise have fallen silent during the active muscle shortening. Only static fusimotor activity could achieve this (Lennerstrand & Thoden, 1968; Matthews, 1972, p. 604). The conclusion that one subset of jaw γ-motoneurones regularly fires in a modulated fashion, whilst the remainder fire tonically, first arose from recordings of γ-axons dissected from masseter nerve in lightly anaesthetized cats (Appenteng, Morimoto & Taylor, 1980; Taylor, Appenteng & Morimoto, 1981). The attribution of the modulated activity to static axons and tonic activity to dynamic axons depended at that time on comparison with spindle afferent recordings made in separate but similar experiments. Later, it was confirmed by simultaneous recordings (Gottlieb & Taylor, 1983) and by stimulation of specific areas of the midbrain (Donga, Taylor & Jüch, 1993; Taylor, Donga &

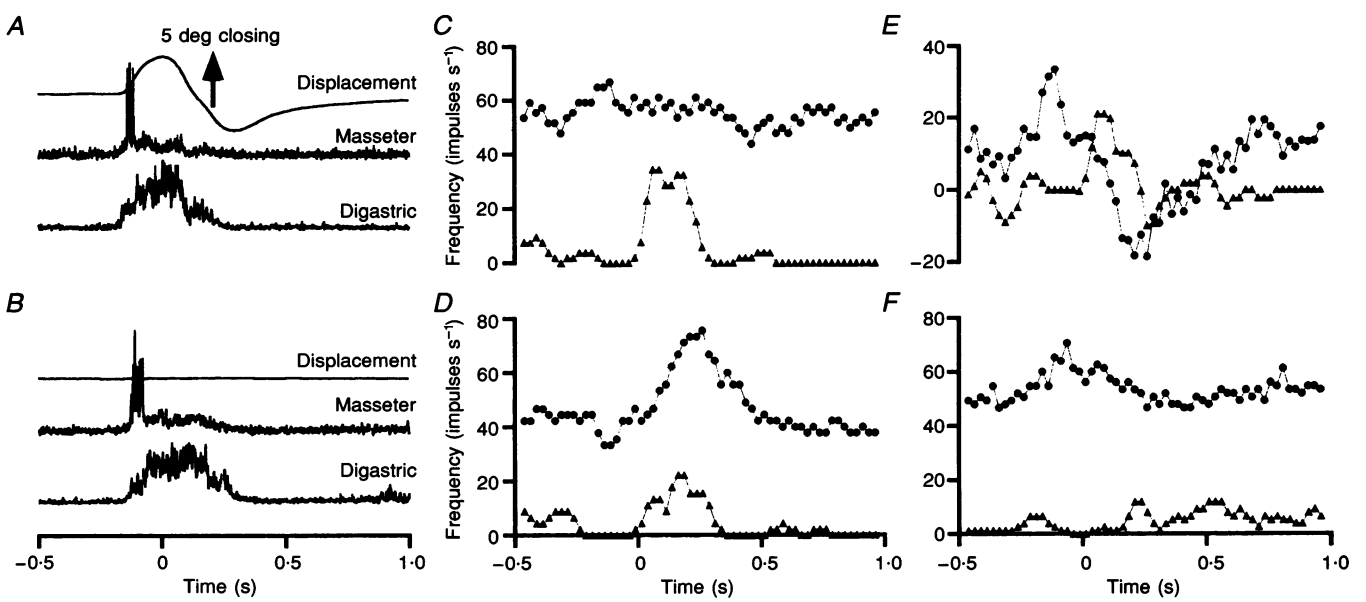

Figure 7. Unloaded and loaded active jaw movements

A, unloaded jaw displacement and rectified masseter and digastric EMG averaged for similar unloaded movements. *B*, averages as in *A*, but with movements obstructed. Records were aligned with respect to the onset of digastric EMG. *C–F*, averaged frequency plots for two spindle afferent units, one being of b_2c type (●), the other b_1b_2c (▲). These records are all aligned with the time scale as in *A* and *B*. *C*, averages from active unloaded movements as in *A*. *D*, effect of the same movements passively applied. *E*, differences of the averaged active and passive responses (*C* − *D*). *F*, averaged frequencies computed from obstructed contractions as in *B*. The number of movements averaged was 7 for *A*, *C*, *D* and *E* and 10 for *B* and *F*.

Jüch, 1993) to identify γ-axons as static or dynamic. These findings are completely consistent with the evidence from chronic recordings of spindle activity in alert cats eating and lapping normally (Taylor & Cody, 1974; Cody, Harrison & Taylor, 1975). The principal effect of anaesthesia appears to be to depress α-activity more than γ-activity, with the result that the reduced and slowed muscle shortening which occurs in the presence of anaesthesia allows the static fusimotor activity to cause an increase in spindle firing during active shortening (Taylor & Appenteng, 1981).

Recordings of jaw muscle spindle afferent activity have also been reported in the monkey (Matsunami & Kubota, 1972; Luschei & Goodwin, 1974; Goodwin & Luschei, 1975). In these cases there appeared to be a variable relationship of fusimotor to α-activity, but without clear conclusions being possible regarding static and dynamic γ-participation. In another study some direct recordings were also made from three γ-motoneurones in the trigeminal motor nucleus (Lund, Smith, Sessle & Murakami, 1979). Two of these showed modulated activity during rhythmical movements while the other was tonically activated. No conclusion could be reached as to their static or dynamic classification, but the substantial increases in spindle secondary afferent firing shown during a biting task strongly suggest that static fusimotor activity started just before the bite and continued at a high level during the maintenance of force. It was an interesting feature that spindle afferents, including secondaries, showed an abrupt cessation of firing at the end of the bite, though the muscle would have been starting to lengthen at that time. This is comparable to the fall in frequency seen during lengthening in the present recordings from b_2c afferents. Evidently the cessation of static fusimotor discharge has a strong tendency to silence spindle secondary afferents.

Natural fusimotor patterns have also been studied in detail for locomotor activity in the cat. Some of the earliest observations of spindle discharge in hindlimb and forelimb muscles in decerebrate animals (Perret & Busser, 1972; Perret & Berthoz, 1973) strongly suggested the presence of static fusimotor modulation in parallel with α-activity. Later, more detailed studies involving recording from hindlimb extensor γ-axons (Murphy, 1982; Murphy *et al.* 1984; Murphy & Hammond, 1990) or spindles (Taylor, Stein & Murphy, 1985; Bennett, De Serres & Stein, 1996) have supported the idea that one group of γ-motoneurones fires tonically whilst another group fires in a modulated fashion, but identified the latter as dynamic. Evidence from chronic recordings from cat hindlimb spindles has been interpreted as indicating that the observed behaviour could be explained by essentially tonic levels of static and dynamic fusimotor firing, though with the possibility of some additional static modulation approximately in parallel with α-activity (Prochazka *et al.* 1987). Another source of similar data was more strongly supportive of there being such modulated static fusimotor drive (Loeb, Hoffer & Pratt, 1985). Recently, further recordings from γ-motoneurones in decerebrates have been taken to favour a modulated static discharge in hindlimb flexors (Murphy & Hammond, 1993). It is possible that the differences between the various studies may reflect real differences in the strategy of use of the γ-motor system in different muscles groups and tasks. The possible effects of anaesthesia or decerebration must also be considered as well as the validity of the various methods used for the interpretation of spindle recordings or the identification of γ-motoneurones as static or dynamic. Perhaps the safest conclusion at the moment is that hindlimb studies offer some support for the scheme of modulated static and tonic dynamic fusimotor patterns in rhythmic movements as found for the jaws, but that some doubt remains as to the generality of this finding.

As to the functional consequences of the present findings for jaw movement control, the most obvious implications are for the involvement of the monosynaptic stretch reflex. The original concept of the 'length follow-up servo' (Merton, 1953) must clearly be rejected because the fusimotor output is not enough to provide the net excitation of spindle afferents needed in this scheme to drive the muscle shortening reflexly. However, the observed pattern of increasing static fusimotor output accompanying shortening would certainly be appropriate for 'servo assistance' (Matthews, 1972). Any loading which slowed the expected shortening would cause a marked increase in spindle afferent firing, which would reflexly compensate for the loading. The idea has been advanced before that the patterned discharge of the static fusimotor firing might represent a 'temporal template' of the intended movement (Taylor *et al.* 1981), such that departure of an actual movement from it would lead to reflex correction. It would be very interesting to know whether changing the background tonic dynamic fusimotor activity would change the afferent response of primary endings to any mismatch between the 'temporal template' and the actual movement.

It has become clear that the monosynaptic stretch reflex is not usually strong enough to provide very effective load compensation. The alternative mechanism, which now has to be considered, is the disynaptic pathway involving convergence of Ia and Ib afferents from hindlimb muscles (Jankowska, Johannisson & Lipski, 1981; McCrea, Schefchyk, Stephens & Pearson, 1995), which under suitable conditions can give powerful excitation of synergist motoneurones. If an equivalent system exists for jaw motor control it might involve convergence of periodontal and spindle afferents to provide strong support for the generation of biting forces through a mixture of positive and negative feedback (see also Lund & Lamarre, 1973). The other use to which spindle feedback might be expected to contribute is in the matching of the central pattern generator's rhythm to that of the part being moved. For this purpose the spindle secondary endings appear to be particularly important (Perreault, Angel, Guertin &

McCrea, 1995; Schomburg, Petersen & Steffens, 1996) and the afferent information from them may therefore be more relevant to this function than to load compensation.

Appenteng, K., Morimoto, T. & Taylor, A. (1980). Fusimotor activity in masseter nerve of the cat during reflex movements. *Journal of Physiology* **305**, 415–431.

Bennett, D. J., De Serres, S. J. & Stein, R. B. (1996). Regulation of soleus muscle spindle sensitivity in decerebrate and spinal cats during postural and locomotor activities. *Journal of Physiology* **495**, 835–850.

Cody, F. W. J., Harrison, L. M. & Taylor, A. (1975). Analysis of activity of muscle spindles of jaw-closing muscles during normal movements in the cat. *Journal of Physiology* **253**, 565–582.

Cody, F. W. J., Lee, R. W. H. & Taylor, A. (1972). A functional analysis of the components of the mesencephalic nucleus of the fifth nerve in the cat. *Journal of Physiology* **226**, 249–261.

Cody, F. W. J. & Taylor, A. (1973). The behaviour of spindles in the jaw-closing muscles during eating and drinking in the cat. *Journal of Physiology* **231**, 49–50*P*.

Crowe, A. & Matthews, P. B. C. (1964). Further studies of static and dynamic fusimotor fibres. *Journal of Physiology* **174**, 132–151.

Donga, R., Taylor, A. & Jüch, P. J. W. (1993). The use of midbrain stimulation to identify the discharges of static and dynamic fusimotor neurones during reflex jaw movements in the anaesthetised cat. *Experimental Physiology* **78**, 15–23.

Goodwin, G. M. & Luschei, E. S. (1975). Discharge of spindle afferents from jaw-closing muscles during chewing in alert monkeys. *Journal of Neurophysiology* **38**, 560–571.

Gottlieb, S. & Taylor, A. (1983). Interpretation of fusimotor activity in cat masseter nerve during reflex jaw movements. *Journal of Physiology* **345**, 423–438.

Jankowska, E., Johannisson, T. & Lipski, J. (1981). Common interneurones in reflex pathways from group Ia and Ib afferents of ankle extensors in the cat. *Journal of Physiology* **310**, 381–402.

Lennerstrand, G. & Thoden, U. (1968). Muscle spindle responses to concomitant variations in length and in fusimotor activation. *Acta Physiologica Scandinavica* **74**, 153–165.

Loeb, G. E. & Hoffer, J. A. (1985). Activity of spindle afferents from cat anterior thigh muscles. II. Effects of fusimotor blockade. *Journal of Neurophysiology* **54**, 565–577.

Loeb, G. E., Hoffer, J. A. & Pratt, C. A. (1985). Activity of spindle afferents from cat anterior thigh muscles. I. Identification and patterns during normal locomotion. *Journal of Neurophysiology* **54**, 549–564.

Lund, J. P. & Lamarre, Y. (1973). The importance of positive feedback from periodontal pressoreceptors during voluntary isometric contraction of jaw closing muscles in man. *Journale de Biologie Buccale* **1**, 345–351.

Lund, J. P., Smith, A. M., Sessle, B. J. & Murakami, T. (1979). Activity of trigeminal α and γ motoneurones and muscle afferents during performance of a biting task. *Journal of Neurophysiology* **42**, 710–725.

Luschei, E. S. & Goodwin, G. M. (1974). Patterns of mandibular movement and jaw muscle activity during mastication in the monkey. *Journal of Neurophysiology* **37**, 954–966.

McCrea, D. A., Schefchyk, S. J., Stephens, M. J. & Pearson, K. G. (1995). Disynaptic group I excitation of synergist ankle extensor motoneurones during fictive locomotion in the cat. *Journal of Physiology* **487**, 527–539.

Matsunami, K. & Kubota, K. (1972). Muscle afferents of trigeminal mesencephalic tract nucleus and mastication in chronic monkeys. *Japanese Journal of Physiology* **22**, 545–555.

Matthews, P. B. C. (1972). *Mammalian Muscle Receptors and their Central Actions*. Edward Arnold, London.

Matthews, P. B. C. (1981). Muscle spindles: their messages and their fusimotor supply. In *Handbook of Physiology*, section 1, *The Nervous System*, part 2, *Motor Control*, ed. Brookhart, J. M. & Mountcastle, V. B., pp. 189–228. American Physiological Society, Bethesda, MD, USA.

Merton, P. A. (1953). Speculations on servo control of movement. In *The Spinal Cord*, ed. Wolstenholme, G. E. W., pp. 247–255. Churchill, London.

Murphy, P. R. (1982). The patterns of discharge of static and dynamic γ-motoneurones in the decerebrate rabbit. *Journal of Physiology* **333**, 29–37.

Murphy, P. R. & Hammond, G. R. (1990). γ-Motoneurone discharge patterns during fictive locomotion in the decerebrate cat. *Experimental Physiology* **75**, 107–110.

Murphy, P. R. & Hammond, G. R. (1993). The locomotor discharge characteristics of ankle flexor γ-motoneurones in the decerebrate cat. *Journal of Physiology* **462**, 59–70.

Murphy, P. R., Stein, R. B. & Taylor, J. (1984). Phasic and tonic modulation of impulse rates in γ motoneurones during locomotion in premammillary cats. *Journal of Neurophysiology* **52**, 228–243.

Perreault, M.-C., Angel, M. J., Guertin, P. & McCrea, D. A. (1995). Effects of stimulation of hindlimb flexor group II afferents during fictive locomotion in the cat. *Journal of Physiology* **487**, 211–220.

Perret, C. & Berthoz, A. (1973). Evidence of static and dynamic fusimotor actions on the spindle response to sinusoidal stretch during locomotor activities in the cat. *Experimental Brain Research* **18**, 178–188.

Perret, C. & Busser, P. (1972). Static and dynamic fusimotor activity during locomotor movements in the cat. *Brain Research* **40**, 165–169.

Prochazka, A. & Hulliger, M. (1983). Muscle afferent function and its significance for motor control mechanisms during voluntary movements in cat, monkey and Man. In *Motor Control Mechanisms in Health and Disease*, ed. Desmedt, J. E., pp. 93–132. Raven, New York.

Prochazka, A., Hulliger, M., Trend, P. & Durmuller, N. (1987). Dynamic and static fusimotor set in various behavioural contexts. In *Mechanoreceptors: Development, Structure and Function*, ed. Hník, P., Soukup, T., Vejsada, R. & Zelena, J., pp. 417–430. Plenum, New York.

Ribot, E., Roll, J. P. & Vedel, J. P. (1986). Efferent discharges recorded from single skeletomotor and fusimotor fibres in man. *Journal of Physiology* **375**, 251–268.

Schomburg, E. D., Petersen, N. & Steffens, H. (1996). On the FRA engagement in spinal locomotor rhythm generation. In *Motor Control VIII*, ed. Gantchev, G. N., Gurfinkel, V. S., Stuart, D. G., Weisendanger, M. & Mori, S., pp. 168–172. Academic Publishing House, Sofia, Bulgaria.

Taylor, A. (1990). *Neurophysiology of the Jaws and Teeth*, Macmillan, London.

TAYLOR, A. & APPENTENG, K. (1981). Distinctive modes of static and dynamic fusimotor drive in jaw muscles. In *Muscle Receptors and Movement*, ed. TAYLOR, A. & PROCHAZKA, A., pp. 172–192. Macmillan, London.

TAYLOR, A., APPENTENG, K. & MORIMOTO, T. (1981). Proprioceptive input from the jaw muscles and its influence on lapping, chewing, and posture. *Canadian Journal of Physiology and Pharmacology* **59**, 636–644.

TAYLOR, A. & CODY, F. W. J. (1974). Jaw muscle spindle activity in the cat during normal movements of eating and drinking. *Brain Research* **71**, 521–530.

TAYLOR, A. & DAVEY, M. R. (1968). Behaviour of jaw muscle stretch receptors during active and passive movements in the cat. *Nature* **220**, 301–302.

TAYLOR, A., DONGA, R. & JÜCH, P. J. W. (1993). Fusimotor effects of midbrain stimulation on jaw muscle spindles of the anaesthetised cat. *Experimental Brain Research* **93**, 37–45.

TAYLOR, A., DURBABA, R. & RODGERS, J. F. (1992*a*). The classification of afferents from muscle spindles of the jaw-closing muscles of the cat. *Journal of Physiology* **456**, 609–628.

TAYLOR, A., RODGERS, J. F., FOWLE, A. J. & DURBABA, R. (1992*b*). The effect of succinylcholine on cat gastrocnemius muscle spindle afferents of different type. *Journal of Physiology* **456**, 629–644.

TAYLOR, J., STEIN, R. B. & MURPHY, P. R. (1985). Impulse rates and sensitivity to stretch of soleus muscle spindle afferent fibers during locomotion in premammillary cats. *Journal of Neurophysiology* **53**, 341–360.

THEXTON, A. J. & MCGARRICK, J. D. (1994). The electromyographic activities of jaw and hyoid musculature in different ingestive behaviours in the cat. *Archives of Oral Biology* **39**, 599–612.

VALLBO, Å. (1985). Proprioceptive activity from human finger muscles. In *Feedback and Motor Control in Vertebrates and Invertebrates*, ed. BARNES, W. J. P. & GLADDEN, M. H., pp. 411–430. Croom Helm, London.

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