J. Physiol. (1975), **253**, *pp.* 565–582
With 10 *text-figures*
Printed in Great Britain

ANALYSIS OF ACTIVITY OF MUSCLE SPINDLES OF THE JAW-CLOSING MUSCLES DURING NORMAL MOVEMENTS IN THE CAT

BY F. W. J. CODY,* LINDA M. HARRISON† AND A. TAYLOR
From the Sherrington School of Physiology,
St Thomas's Hospital Medical School,
London SE1 7EH

(*Received 22 May 1975*)

SUMMARY

1. Recordings have been made of afferent activity from spindles of the jaw-closing muscles, together with jaw movement and e.m.g. from temporalis and masseter in conscious, unrestrained cats.

2. In the twenty-nine units studied, the pattern of spindle behaviour observed during eating and lapping was generally what might be expected of stretch receptors. Maximal firing frequencies were found during opening of the mouth (lengthening), while during active closing the discharge was progressively reduced or abolished. Nevertheless, changes in the relation of stretch to firing frequency in different movements indicated that fusimotor drive was not constant.

3. Spindle afferents could be divided into two groups on the basis of their maximal firing frequency during eating. 'High-frequency' units (range 240–600 impulses/sec) showed pronounced velocity sensitivity, which supports the proposal that they correspond to spindle primaries. 'Low-frequency' units (range 80–200 impulses/sec) showed predominantly length sensitivity and probably correspond to secondary endings.

4. Length sensitivity of low-frequency units was considerably greater in lapping movements than in eating, indicating increased static fusimotor drive in the former. Sensitivity in the opening phase of eating was indistinguishable from that recorded in deeply anaesthetized animals.

5. High-frequency units were generally silenced immediately active shortening commenced.

6. No simple relationship existed between temporalis or masseter e.m.g. and spindle firing.

7. These results imply that normal masticatory movements are not

---

* Present address: Department of Physiology, University of Manchester, Manchester, M13 9PT, England.

† Correspondence to L.M.H.

initiated or driven to any appreciable extent via the fusimotor route. Close α–γ co-activation is not a feature of this situation. On the other hand, in some other movements, such as licking the lips, fusimotor drive could fluctuate so as largely to cancel the unloading effects of active muscle shortening.

INTRODUCTION

It has become clear in recent years that the concept of muscle spindles acting as length feed-back transducers in a servo system driven via the fusimotor route (Merton, 1953) does not lead to a generally satisfactory view of voluntary muscle control. Thus the fusimotor drive, originally thought to be in the form of a 'bias' signal, in fact serves additionally to regulate length and velocity sensitivity (for review, see Matthews, 1972). Furthermore, theoretical arguments have been advanced against the reasons proposed for driving via the fusimotor route (Taylor, 1972; Stein, 1974). On the other hand, the availability of independent adjustment of the static and dynamic characteristics of muscle spindles could in principle confer great flexibility on the feed-back control operating through them. It is evident that for the appropriate adjustment to be carried out continuously via the fusimotor system, there must exist a capability for high-level neural processing. Thus a serious practical difficulty obstructs further investigation of the normal function of muscle spindles, unless experimental situations can be devised to avoid anaesthesia or decerebration, which are bound to disorganize the system being studied.

Two approaches are now available. In man, the work of Hagbarth & Vallbo (1969) and Vallbo (1971, 1973, 1974*a*, *b*) has shown the feasibility of recording from single muscle afferents during limited voluntary movements. In animals, advantage may be taken of the fact that in the special case of the jaw-closing muscles the first-order cell bodies of spindle afferents are located in the mid-brain (Corbin & Harrison, 1940; Cody, Lee & Taylor, 1972) where they are accessible to extracellular microelectrodes. The potentialities of this approach were appreciated some while ago (Davey & Taylor, 1966, 1967; Taylor & Davey, 1968) and initial observations on fully mobile cats reported recently (Cody & Taylor, 1973; Taylor & Cody, 1974). The present work adds some new data and examines in more detail the ways in which muscle spindles may control these particular movements.

METHODS

Young adult cats of either sex, weighing 2·5–3·5 kg were chosen for their calm and friendly disposition. Fig. 1 is a diagram of the attachments used for recording.

Surgery. At one aseptic operation under pentobarbitone anaesthesia (35 mg/kg

I.P.) implants were made of e.m.g. electrodes, fittings for the jaw movement transducer and a chamber for attachment of the micro-electrode drive. This chamber was a Perspex cylinder (10 mm diameter, 15 mm height centred on the stereotoxic vertical axis 3·0 mm rostral and 2·3 mm lateral over a hole (5 mm diameter) drilled through the calvarium. It was secured by four stainless-steel screws and acrylic cement and closed with an airtight cap. Two 1 mm sockets soldered to the caudal pair of screws served as the recording earth and for the attachment of the FET micro-electrode pre-amplifier.

E.m.g. electrodes were pairs of enamelled silver wires with their terminal 4 mm bared, hooked and inserted into the temporalis and masseter with a syringe needle. They were intended to record large scale representative electrical activity. Connexion was made via a miniature socket attached to the front of the micro-electrode chamber.

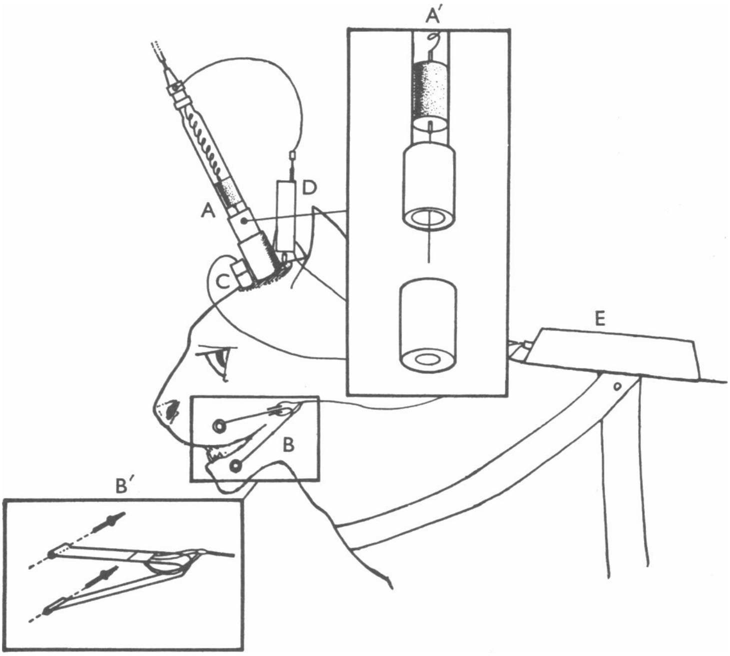

Fig. 1. Diagram of the recording devices carried by the cat. A, micro-electrode drive, shown enlarged in inset A′. B, jaw movement transducer, shown enlarged in inset B′. C, connector for e.m.g. D, FET input stage for micro-electrode. E, pack containing e.m.g. amplifiers and connectors for micro-electrode and transducer amplifiers.

Jaw movements were recorded with a very compliant strain-gauge (Taylor, 1969). For this purpose, two stainless-steel screws (6 mm length, countersunk heads 4 mm diameter) were inserted, one into the maxilla and one into the mandible on one side. Each screw had a stainless-steel rod set into its head so as to protrude laterally 10 mm through the skin. Such screws were well tolerated and could remain in position for 2 or more weeks.

Unitary recording. Glass-covered tungsten micro-electrodes (Merrill & Ainsworth, 1972) were used with impedance of 1–3 MΩ at 1·7 kHz. The drive was a simple hydraulic system comprising two precision bore syringes (Agla, Burroughs-Wellcome) connected by 60 cm of nylon tubing and filled with liquid paraffin. One syringe was operated by a micrometer drive and the other was shortened to 6 cm to fit into the skull chamber. The shortened piston of this syringe was drilled axially and a length of hypodermic needle tubing cemented in place. The micro-electrode butt was mounted in this slightly eccentrically, so that by rotating the syringe a series of tracks could be made on the periphery of a circle of about 0·5 mm radius. The Perspex skull chamber had a vertical internal groove to allow for escape of air when the electrode holder was fitted.

The scalp wound was sutured around the skull fittings and dressed with collodion and gauze. Penicillin was administered post-operatively. Recording sessions could start 3 days later and generally two electrode tracks were made in each session. Jaw movement, temporalis and masseter e.m.g. and spindle unit activity were recorded on FM magnetic tape with 2·5–5 kHz bandwidth (Philips: Analog 7).

Identification of spindle units. The feasibility of the present approach depends on the prior work on the mesencephalic nucleus of the 5th nerve in the cat under anaesthesia (see Cody *et al.* 1972) which demonstrated the functional constituents of the nucleus to be 1st order afferents for jaw-closing muscle spindles and dental mechano-receptors. Subsequently (Cody, Harrison, Taylor & Weghofer, 1974) the dental receptors were found to be restricted to the caudal part of the nucleus. In its rostral part the nucleus consists of only a thin scattering of large cells on the dorsolateral aspect of the central grey matter within a rostro-caudal strip about 1·5 mm wide and 4·5–5 mm below the surface of the superior colliculus. Penetration of the latter structure by the electrode was marked by the onset of plentiful unitary activity related to movement in the visual field. Further penetration with the electrode then encountered a relatively silent region with isolated units firing in relation to jaw movement to be found at the expected depth for the nucleus or not at all. Recordings are presented from those units which could be activated by local pressure on the masseter or temporalis as previously described in anaesthetized cats and by passive jaw opening. The arguments for regarding these as belonging to spindle and not to joint or other receptors are given by Cody *et al.* (1972).

RESULTS

Recordings have been obtained from twenty-nine units belonging to spindles in the jaw-closing muscles of five cats. Simultaneous recordings of jaw movement and of temporalis and masseter e.m.g. were available in twenty-two cases and of e.m.g. only in seven others. When movement records could not be made, the e.m.g. traces were used to indicate the timing of opening and closing during eating and lapping. The food offered was commercial canned meat of generally soft uniform consistency.

Examples of recording of the four variables are shown in Figs. 2 and 3. In the cat, masticatory movements are essentially those of a simple hinge at the temporo-mandibular joint. During lapping they showed particularly repeatable cycles at approximately 3·5 Hz, disturbed every 4 or 5 cycles by a swallowing movement. During eating, opening occurred in two phases; an initial slow component of some 10° lasting 100–150 msec, followed by a rapid one of 15–20° in 50–75 msec. Closing on solid food showed three phases. A large, quick component was followed by a small continued closing, terminated by a further rapid small movement. This led directly into the first phase of opening. E.m.g. records, shown particularly clearly in Fig. 2*A*, revealed a single phase of activity in temporalis during closing. Masseter, on the other hand, normally gave an additional burst in the final quick phase of closing continuing well into the first phase of opening.

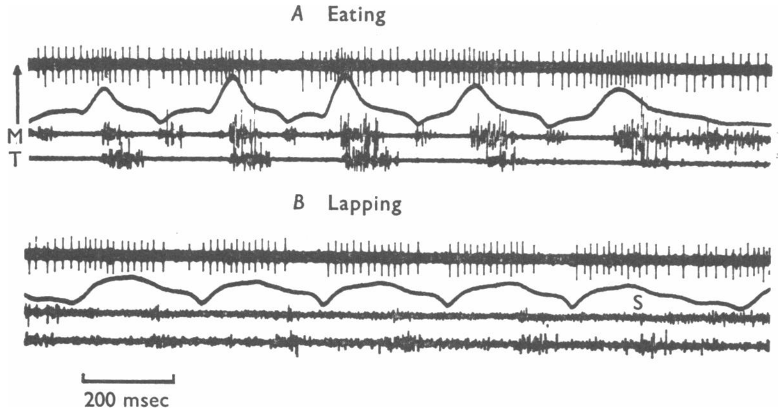

Fig. 2. Responses of a 'low-frequency' spindle unit in masseter during eating and lapping. The arrow represents 25° of jaw opening. E.m.g. (same gain throughout) was recorded from masseter (M) and temporalis (T). Swallowing is indicated by S in record *B*.

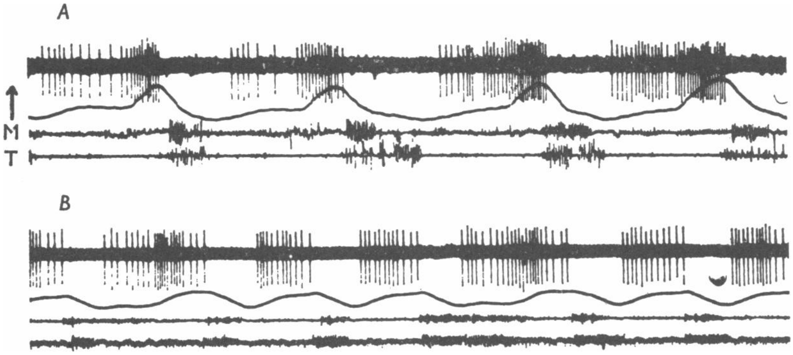

Fig. 3. Responses of a 'high-frequency' masseter unit during eating and lapping. Labelling as in Fig. 2.

Typically, spindle discharge increased during opening movements (increased muscle length) while during active shortening, firing was reduced or silenced. As indicated previously (Taylor & Cody, 1974), it appears that the spindle afferents may be classified according to their maximal firing frequencies seen during natural masticatory movements.

Fig. 4 shows data summarized for all units in the form of histograms of average maximum instantaneous frequency (MIF) attained during 10 similar movement cycles. It is evident that, while during lapping (*B*) the MIF in all but one case lay between 40 and 200 impulses/sec the larger movements of eating (*A*) drove ten out of the twenty-four units to much higher frequencies. Thus, the units may be divided into a low-frequency group with MIF up to 200 impulses/sec and a high-frequency group with MIF of 240 impulses/sec and above. That this is a significant division was supported by the observation that the high-frequency units were very phasic in their behaviour, being most often completely silent during muscle shortening (Fig. 3) whereas the low-frequency units (Fig. 2) were relatively less phasic. Observations on the jaw-muscle spindle afferents in anaesthetized cats (Cody *et al.* 1972) have shown that units could be divided into two approximately equal groups according to dynamic index during passive ramp stretches, provided that the spindles were activated by succinyl choline. The implication was that the higher dynamic index units belonged to primary endings and it seems likely that these correspond to the present

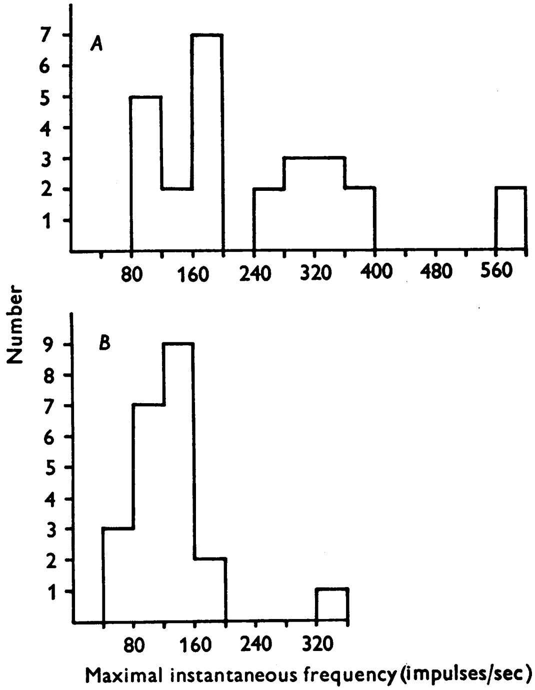

Fig. 4. Histograms of maximum instantaneous frequency of spindle discharge (MIF) found as the average values in ten successive cycles of eating (*A*) and lapping (*B*).

high-frequency units. However, recognizing that the evidence for their identification is incomplete, we shall retain for the moment the descriptive terms of 'high-' and 'low-frequency' units.

Low-frequency units. Fourteen units were classified as 'low frequency' according to the above criteria. A further two units, for which recordings were obtained during lapping only, were included in this category on the basis of their firing patterns. The impression of predominantly static length sensitivity of low-frequency units illustrated in Fig. 2 is emphasized by the computer plot of instantaneous frequency and jaw movement in Fig. 5. It is clear that firing frequency increases progressively during jaw opening and decreases during active closing. The 'frequencygrams' show a striking parallelism between the unit frequency and the jaw position. It is particularly noteworthy that despite the large range of the movements

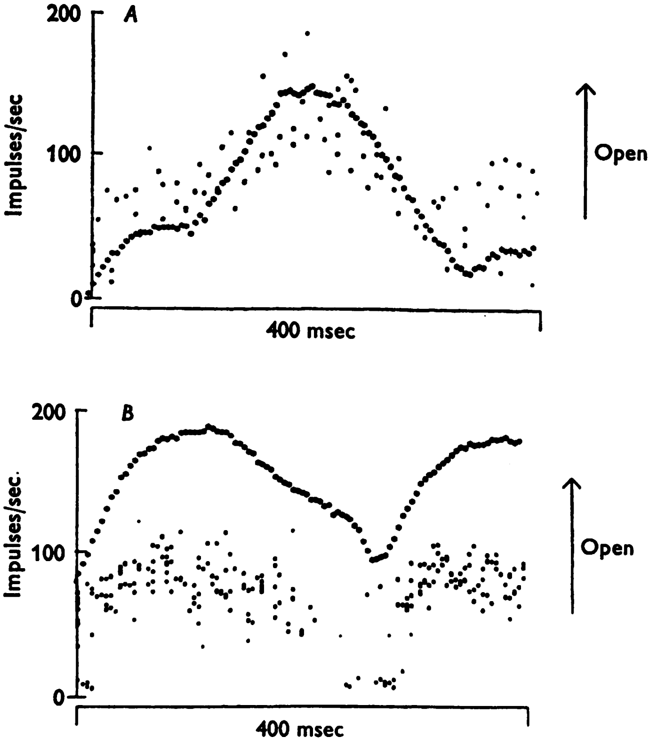

Fig. 5. Time course of jaw movement and frequency of firing of 'low-frequency' unit in temporalis muscle during eating (*A*) and lapping (*B*). The heavy dotted line is the average movement estimated in 5 cycles. The fine dots are superimposed instantaneous frequency points from the same 5 cycles. The vertical arrow indicates 25° in *A* and 10° in *B*.

occurring, the relationship of frequency to length appears to be essentially identical in the lengthening and the shortening phases. It should be pointed out that the variability of frequency in relation to length in this plot may be more apparent than real. The movement record is averaged over 10 cycles, but the individual instantaneous frequency values are all displayed without averaging. Thus, some of the variability in frequency at each point in the cycle will represent variability of movement between cycles. Nevertheless, plotting a scatter diagram of frequency against position for low-frequency units over 5 cycles as in Fig. 6 reveals a highly significant positive correlation and no suggestion that a curvilinear relation would be more appropriate than a straight line. This result was confirmed in five units during five to eight masticatory cycles in each case.

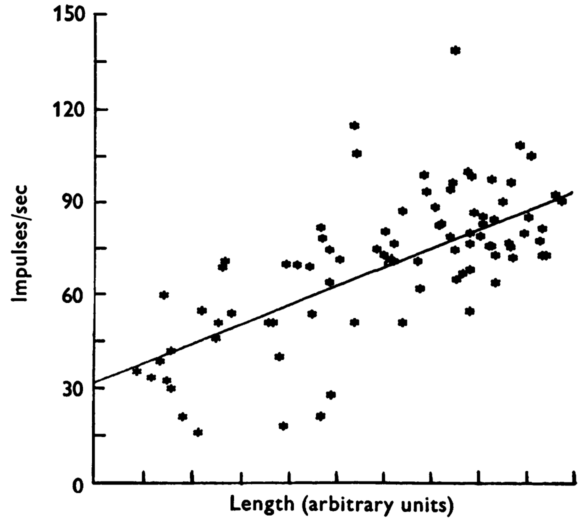

Fig. 6. Plot of instantaneous frequency of firing for 'low-frequency' temporalis unit of Fig. 5. Data are derived from 5 cycles. Correlation coefficient 0·678, 85 points, $t = 8·4$.

If there were any appreciable dynamic sensitivity during the course of these movements, plots of frequency against length would be expected to open into loops, with higher frequencies at any given length during opening than during closing. That this is not the case is demonstrated in Fig. 7 where instantaneous frequency points during opening and closing are distinguished. Attention is particularly drawn to the fact that the slope of the relationship is much greater during lapping than during eating, the respective values in these single cycles being 11·98 and 4·18 impulses/sec. deg. Data for three low-frequency units for which good eating and lapping records were available are summarized in Table 1. This description fitted the majority of low-frequency units, but in three instances, appreciable dynamic sensitivity was observed.

It is thus possible to summarize the behaviour of the majority of low-frequency spindle afferents in the jaw-closing muscles as essentially that of length transducers whose sensitivity may be changed according to the type of movement cycle being performed.

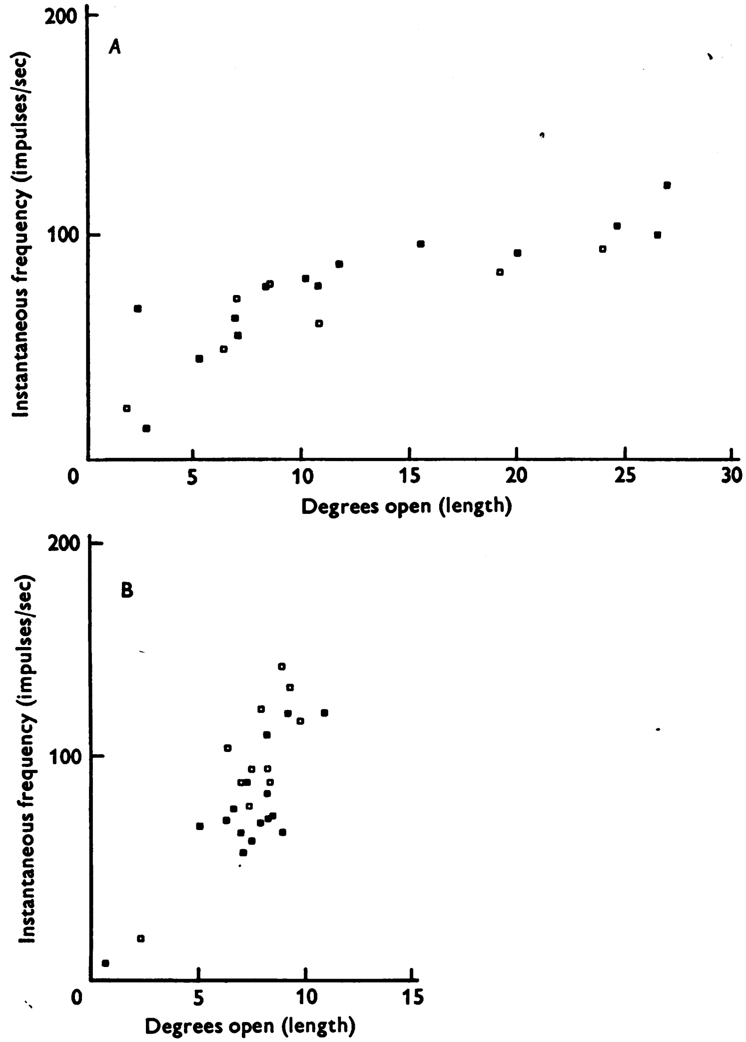

Fig. 7. Plots of instantaneous frequency of firing for single cycles of eating (*A*) and lapping (*B*). Same unit as in Fig. 5. Frequency points arising during mouth opening are shown by ■ and during closing by □.

High-frequency units. This group comprised thirteen units. Their discharge (e.g. Fig. 3) was phasic with the highest frequencies reached during jaw opening. Closing was accompanied by very marked reduction in firing or by complete silencing of the unit. Such units were far more sensitive to local pressure than were the low-frequency units, so that their muscle of origin could be identified with greater certainty.

TABLE 1. Comparison of sensitivity of low-frequency spindle units to stretch during eating and lapping movements. Stretch is measured in degrees of angular opening of the jaw

Unit	MIF in eating (impulses/sec)	Sensitivity eating (impulses/sec.deg)	Sensitivity lapping (impulses/sec.deg)
1	200	7·2	11·6
2	150	4·2	13·2
3	150	4·2	11·4

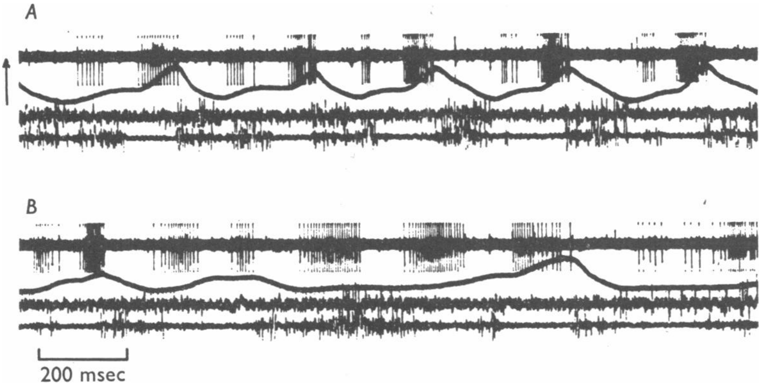

Fig. 8. Responses of an extremely phasic 'high-frequency' temporalis unit. Labelling as in Fig. 2.

Five units, exemplified by Fig. 8 appeared to be almost exclusively velocity sensitive. The two high-frequency bursts during eating movements (Fig. 8*A*) corresponded to the two phases of opening. Length sensitivity seemed to be relatively unimportant. This is emphasized by the plot in Fig. 9 of instantaneous frequency against velocity for five chewing cycles for another similar unit.

It is evident that, although particular velocities of stretch could occur over a range of different lengths, the observed instantaneous firing frequencies could be well described as bearing a linear relation to velocity. In only two cases of high-frequency units were the recordings in both eating and lapping of adequate quality to permit comparison of sensitivity. For the unit of Fig. 9 velocity sensitivity was 0·6 and 0·5 impulses/deg in eating and lapping respectively and for the other unit 0·3 and 0·5 impulses/deg respectively (impulses per sec per degree per sec = impulses/deg).

Though it is true that during regularly repeating cycles of eating and lapping there was a reasonably constant relationship between velocity and firing frequency, in other segments of recording this did not hold, as exemplified by Fig. 8 *B*. Here it is seen that large bursts could occur during small slow opening movements. Clearly, there must be greatly enhanced fusimotor drive at these firings, which is not clearly related to e.m.g. activity.

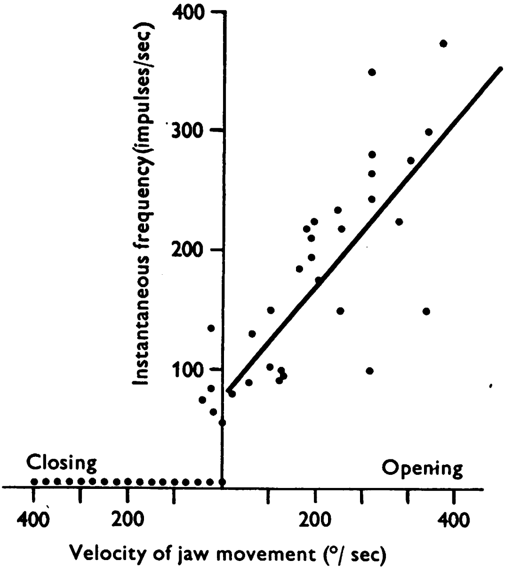

Fig. 9. Plot of instantaneous frequency of firing against velocity of jaw movement for a 'high-frequency' temporalis unit. The dots at zero frequency during the closing phase indicate that velocity measurements were made at these points but no discharge occurred. Data from a single cycle of eating.

Other jaw movements. Occasionally the opportunity arose for recording spindle activity in other large scale but less repetitive movements such as licking the lips. Two single unit records were obtained in this situation and both were from high-frequency units. One was of the highly phasic type and the other of the type with relatively less velocity sensitivity. It was conspicuous that during the closing phase of this movement the spindles were silenced much less than was usual during eating despite the fact that movements were of similar size and the closing velocities not much less. In the case of the less velocity-sensitive unit (Fig. 10) the firing frequency was held almost constant during opening and closing movements of 25° extent. This must mean that under some conditions fusimotor drive can fluctuate rapidly enough to keep up with extrafusal muscle shortening. However, even in this case fusimotor drive did not lead the movement so as to cause spindle acceleration during active shortening.

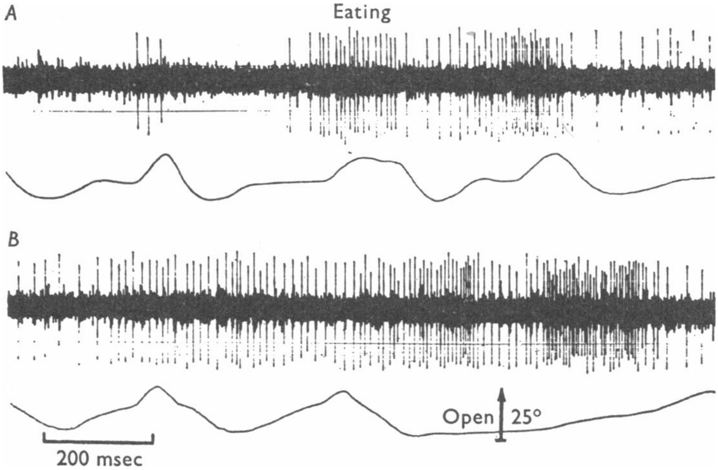

Fig. 10. Responses of a 'high-frequency' unit from temporalis during eating (A) and during licking the lips (B). In B, frequency can remain quite constant despite large movements.

Relation of spindle sensitivity in conscious animals to that in deep anaesthesia. In order to interpret the above results it would clearly be desirable to know the behaviour of the individual spindle afferents in the complete absence of fusimotion. Since this information was not directly available, a series of experiments was performed on five cats deeply anaesthetized with pentobarbitone and chlorpromazine to suppress fusimotor activity (briefly reported by Cody & Harrison, 1975). Natural jaw movements of eating and lapping, previously recorded on magnetic tape, were played back through an electromagnetic servo attached to the mandible so as to reproduce them exactly. In the sample of forty-five spindle afferents all units were silenced during the whole of the closing phase of both passive eating and lapping. Though there was a wide range of dynamic sensitivities, it was not possible to distinguish two populations on this basis corresponding to primary and secondary spindle endings. This is in confirmation of the previous findings under similar conditions with ramp stretches (Cody *et al.* 1972), recognizing that, in that work, differentiation was made possible by the injection of succinyl choline to activate intrafusal fibres. In the present series of anaesthetized animals, dynamic index and MIF were well correlated, but the MIF (range 80–290) was never as great as the highest values attained in the conscious animals (range 80–600). This is suggestive evidence of the occurrence of dynamic fusimotor activation during the natural masticatory movements. It was also found that the length sensitivity of the low-frequency units to passive stretch was essentially the same as that during the active eating movements, but with the difference that even the low-frequency units were silenced from the beginning of shortening in the anaesthetized animals. This can only be explained as indicating absence of static fusimotion during the opening phase of active eating and some increase during the closing phase.

DISCUSSION

The present experimental approach has made available data on the normal behaviour of muscle spindles in the cat in the particular motor control situation of eating and lapping movements. The significance of the results will be discussed first in relation to other comparable data and secondly to see whether any conclusions can be extended to movement control in general.

The most comparable previous experiments are those of Matsunami & Kubota (1972), who recorded from cells in the mid-brain of the monkey restrained by a head clamp. In this preparation, the relationship between presumed spindle afferent units and e.m.g. was variable. Half the units observed were said to increase their frequency during contraction while the others showed reduced activity. The former behaviour is quite different from that seen here and the reason for the difference is not clear. However, Matsunami & Kubota did not make jaw movement recordings simultaneously with unit recordings. Instead they related masseter e.m.g. to uncalibrated jaw acceleration traces then related unit discharge to the masseter e.m.g. in separate experiments. In the cat we find that masseter commonly has two periods of activity: the main one during closing and a second smaller burst immediately before and at the beginning of the opening phase. In the absence of continuous jaw displacement records, therefore, uncertainties of timing could arise. In any case the mechanical situation is much more complex in the monkey (Luschei & Goodwin, 1974) which has considerably more lateral mobility of the jaw than has the cat in which the temporo-mandibular joint is essentially a hinge. The other point which makes the monkey a relatively unsuitable animal for this work at present is the lack in that species of any detailed study of the mesencephalic nucleus of the fifth nerve, whereas in the cat, a body of work has now established the physiological constitution of the nucleus (Corbin & Harrison, 1940; Jerge, 1963; Cody *et al.* 1972, 1974). Previous work on the lightly anaesthetized cat (Davey & Taylor, 1966; Taylor & Davey, 1968) indicated the occurrence of variable fusimotor drive during the course of reflex jaw movements but no serious attempts were made to interpret the results because it was appreciated that the motor system was likely to be disordered by even small doses of anaesthetic. It may be inferred from some of these published observations (Taylor & Davey (1968), fig. 2) that there is not a fixed relationship between fusimotor and α-motor drive and this is also a conspicuous feature of the present results in the conscious animal. Thus, some of the time, spindles seem to behave as passive stretch receptors with their sensitivity set to a value appropriate to the scale of movement being performed, while on other occasions (e.g. during licking of the lips) fusimotor drive appears to fluctuate so as to keep firing rate remarkably constant during large movements. Even here, however, jaw-closing muscle spindles never increased their frequency during active muscle shortening. On this basis, we may be confident that the jaw movements are not initiated and continued via the fusimotor route in the way proposed by the original 'length follow up servo' idea (Merton, 1953), because this would have required that the shortening should result from the excitatory effect of increased spindle afferent activity.

Another experimental area with which the jaw movement work may well be compared is that of the respiratory muscles. It seems likely, because of the relative resistance of rhythmic respiration to anaesthesia and the repeatability of the results which may be obtained in anaesthetized animals, that such results may well be close to normal. A series of papers have appeared on this subject from Sears and from von Euler and their respective collaborators and have been reviewed recently by Granit (1970) and by Sears (1973). In the intercostal muscles, co-activation appears to be the rule. Indeed, the fusimotor drive to a particular segment of muscle is generally more than enough to prevent unloading and there is a net excitation of the spindle during active shortening. Hence in this case, since there is clear evidence of excitatory synaptic connexion to the motoneurones (Eccles, Sears & Shealy, 1962) the fusimotor drive may make a substantial contribution to the extrafusal contraction.

Of great interest also, because of spindle recordings made without anaesthesia is the work of Severin, Orlovskii & Shik (1967) on locomotion in the high decerebrate cat. Despite difficulties in interpretation due to the non-quantitative movement recordings and problems in characterization of receptors, it is clear that co-activation of α and fusimotor neurones did occur. Thus in ankle extensors, there was marked spindle discharge during the stance phase of walking extending from the active lengthening into the active shortening periods. Very little firing occurred in the passive lengthening caused by antagonists during the swing phase. This is in marked contrast with the jaw movement records in which the spindles are active essentially during the passive lengthening phase.

The human observations by Hagbarth & Vallbo (1969) and by Vallbo (1971, 1974*a*, *b*) have concentrated on the relation between spindle discharge and α motor activity during voluntary isometric contractions. The isometric situation was largely dictated by the micro-neurographic technique, but had the potential advantage that, in the absence of extrafusal muscle length changes, the spindle afferent discharge should be a reliable measure of fusimotor drive. The general conclusion reached (Vallbo, 1974*a*, *b*) was that during isometric voluntary contractions, there is strong static and dynamic fusimotor co-activation. There is a restrictive feature of this approach however, in that as length receptors the spindles are unlikely to be of great value in the control of isometric contractions. Thus it would be unwise to seek to apply such results directly to movement control, as they imply lack of the flexibility which the dual independent fusimotor system would be expected to provide.

In relation to these other various approaches to muscle spindle function the present results on jaw movements should not be seen as contradictory but as supplementary. We find that in the rapid repetitive large scale movements of lapping and eating, fusimotor action is such as to make the spindles appear as passive stretch receptors with adjustable sensitivity. They can on occasion be driven via the fusimotor system to keep their frequency remarkably constant despite large length changes but they do not apparently show net excitation during active shortening. Such results might be interpreted first from the point of view of deducing the underlying pattern of fusimotor activity and secondly to consider in what way the nervous system may be using the observed spindle afferent inflow in regulating movements.

It should be possible to deduce the form of the static fusimotor drive from the behaviour of the secondary spindle afferents, since they are unaffected by dynamic fusimotor activity (Jansen & Matthews, 1962; Matthews, 1972, p. 253). The firing of the majority of the 'low-frequency' (presumably secondary) units was closely related to muscle length with the slope of frequency to displacement equal during passive lengthening and active shortening but greater in lapping than in eating. The simplest basis for this would be constant static fusimotor drive throughout the cycle, at a higher level (to give higher incremental displacement sensitivity) in lapping than in eating. However, a puzzling finding was that presumably full suppression of fusimotor activity with anaesthesia caused all spindles to be silenced during the whole of passively applied shortening. By contrast, in the conscious cat, in eating movements in which incremental stretch sensitivity during opening was the same as in anaesthesia, firing of low frequency units persisted into closing. It thus seems likely that static fusimotor drive can be low or absent during the muscle lengthening phase and yet be enhanced during shortening so as to give the same apparent relationship of firing frequency to length in the two phases.

The apparent static sensitivities seen here are high but not unreasonably so in relation to results reported on cat hind-limb muscles. Thus Brown, Lawrence & Matthews (1969) report mean increases of sensitivity of spindle secondary endings to triangular stretch from 8 impulses/sec.mm without fusimotor stimulation to 28 impulses/sec.mm with combined stimulation of several ventral root filaments at 150/sec. Static fusimotor excitation also has a powerful biasing effect and it is worth noting that the mean frequency of the unit of Fig. 5 is considerably higher during lapping than in eating, which is consistent with higher fusimotor activation in the former case.

As regards the apparent primary ('high-frequency') units, their discharge is more difficult to interpret since if they do belong to primary endings it would depend on static and dynamic fusimotor drive and length and velocity of stretch. At this stage the data do not permit us to make any definite statement about the changes in dynamic fusimotor drive during eating and lapping.

The general conclusion which arises from this work is that rigid co-activation is not a feature of this particular movement system. Rather, during lapping and eating, fusimotor drive seems to operate to make the primary and secondary afferents behave essentially as velocity and length transducers respectively. This does not in itself preclude the possibility of the involvement of the spindle afferents in a length servo control system. It was pointed out by Matthews (1964) and has been re-emphasized recently (Taylor, 1972; Stein, 1974) that the advantages of servo control are retained if the drive is entirely via the α motoneurones, provided that enough fusimotion exists to prevent silencing of the spindles during shortening, which would effectively open the control loop. In point of fact, the 'primary' afferents have been shown to be silenced for most of the jaw-closing phase so that they cannot be regarded as linear feed-back devices for length control via the classical stretch reflex. On the other hand, the presumed secondary afferents, though clearly unloaded by active shortening, commonly fire to some extent throughout the active contraction, particularly in eating. There is still some dispute regarding the reflex effects of spindle secondaries but evidence now exists (Matthews, 1969, 1970; Kirkwood & Sears, 1974) which strongly supports the contention that they can cause substantial autogenetic excitation. Thus it seems that a theoretical case can be made for the possibility of some degree of length servo operation in eating movements, but qualitative examination of the e.m.g. and spindle record does not indicate that any marked degree of load compensation is occurring.

Very much the same conclusion was reached by Goodwin & Luschei (1974) studying the effects of lesions of the tract of the mesencephalic nucleus of the fifth nerve in monkeys. These authors have also recently made recordings from the mesencephalic nucleus in monkeys (personal communication) and while not attempting to separate primary and secondary responses, found that all spindle afferents decreased their firing during active shortening.

It would now be desirable to have further quantitative analyses of spindle activity in jaw movements in the cat with some means of making unexpected small changes in loading during the course of normal movements. Furthermore, the understanding of the results of this type of approach would be greatly facilitated if we had more knowledge of the strength of the reflex connexions of the muscle afferents and of how it may be modified during normal movements.

This work was supported in its early stages by the National Fund for Research into Crippling Diseases and subsequently by the Medical Research Council.

REFERENCES

Brown, M. C., Lawrence, D. G. & Matthews, P. B. C. (1969). Static fusimotor fibres and the position-sensitivity of muscle spindle receptors. *Brain Res.* **14**, 173–187.

Cody, F. W. J. & Harrison, L. M. (1975). Responses of cat jaw muscle spindles to passive stretching over the masticatory range. *J. Physiol.* **245**, 67–68*P*.

Cody, F. W. J., Harrison, L. M., Taylor, A. & Weghofer, B. (1974). Distribution of tooth receptor afferents in the mesencephalic nucleus of the fifth cranial nerve. *J. Physiol.* **239**, 49–51*P*.

Cody, F. W. J., Lee, R. W. H. & Taylor, A. (1972). A functional analysis of the components of the mesencephalic nucleus of the fifth cranial nerve in the cat. *J. Physiol.* **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. *J. Physiol.* **231**, 49–50*P*.

Corbin, K. B. & Harrison, F. (1940). Function of the mesencephalic root of the fifth cranial nerve. *J. Neurophysiol.* **3**, 423–435.

Davey, M. R. & Taylor, A. (1966). Activity of cat jaw muscle stretch receptors recorded from their cell bodies in the mid-brain during spontaneous jaw movements. *J. Physiol.* **185**, 62–63*P*.

Davey, M. R. & Taylor, A. (1967). The activity of jaw muscle spindles recorded together with active movement in the cat recovering from anaesthesia. *J. Physiol.* **190**, 8–9*P*.

Eccles, J. C., Sears, T. A. & Shealy, C. N. (1962). Intracellular recording from respiratory motoneurones of the thoracic spinal cord. *Nature, Lond.* **193**, 844–846.

Goodwin, G. M. & Luschei, E .S. (1974). Effects of destroying the spindle afferents from the jaw muscles upon mastication in monkeys. *J. Neurophysiol.* **37**, 967–981.

Granit, R. (1970). *The Basis of Motor Control*. London: Academic Press.

Hagbarth, K.-.E. & Vallbo, Å. B. (1969). Single unit recordings from muscle nerves in human subjects. *Acta physiol. scand.* **76**, 321–334

JANSEN, J. K. S. & MATTHEWS, P. B. C. (1962). The effects of fusimotor activity on the static responsiveness of primary and secondary endings of muscle spindles in the decerebrate cat. *Acta physiol. scand.* **55**, 376–386.

JERGE, C. (1963). Organisation and function of the trigeminal mesencephalic nucleus. *J. Neurophysiol.* **26**, 379–392.

KIRKWOOD, P. A. & SEARS, T. A. (1974). Monosynaptic excitation of motoneurones from secondary endings of muscle spindles. *Nature, Lond.* **252**, 243–244.

LUSCHEI, E. S. & GOODWIN, G. M. (1974). Patterns of mandibular movement and jaw muscle activity during mastication in the monkey. *J. Neurophysiol.* **37**, 954–966.

MATSUNAMI, K. & KUBOTA, K. (1972). Muscle afferents of trigeminal mesencephalic tract nucleus and mastication in chronic monkeys. *Jap. J. Physiol.* **22**, 545–555.

MATTHEWS, P. B. C. (1964). Muscle spindles and their motor control. *Physiol. Rev.* **44**, 219–288.

MATTHEWS, P. B. C. (1969). Evidence that the secondary as well as the primary endings of the muscle spindles may be responsible for the tonic stretch reflex of the decerebrate cat. *J. Physiol.* **204**, 365–393.

MATTHEWS, P. B. C. (1970). A reply to criticism of the hypothesis that the group II afferents contribute excitation to the stretch reflex. *Acta physiol. scand.* **79**, 431–433.

MATTHEWS, P. B. C. (1972). *Mammalian Muscle Receptors and Their Central Actions*. London: Arnold.

MERRILL, E. G. & AINSWORTH, A. (1972). Glass-coated platinum-plated tungsten microelectrodes. *Med. biol. Engng* **10**, 662–671.

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

SEARS, T. A. (1973). Servo-control of intercostal muscles. In *New Developments in Electromyography and Clinical Neurophysiology*, vol. 3, ed. DESMEDT, J. E., pp. 404–417. Basel: Karger.

SEVERIN, F. V., ORLOVSKII, G. N. & SHIK, M. L. (1967). Work of the muscle receptors during controlled locomotion. *Biophysics* **12**, 575–586.

STEIN, R. B. (1974). Peripheral control of movement. *Physiol. Rev.* **54**, 215–243.

TAYLOR, A. (1969). A technique for recording normal jaw movements in conscious cats. *Med. biol. Engng* **7**, 89–90.

TAYLOR, A. (1972). Muscle receptors in the voluntary control of movement. *Paraplegia* **9**, 167–172.

TAYLOR, A. & CODY, F. W. J. (1974). Jaw muscle spindle activity in the cat during normal movements of eating and drinking. *Brain Res.* **71**, 523–530.

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

VALLBO, Å. B. (1971). Muscle spindle response at the onset of isometric voluntary contractions in man. Time difference between fusiomotor and skeletomotor effects. *J. Physiol.* **218**, 405–431.

VALLBO, Å. B. (1973). Muscle spindle afferent discharge from resting and contracting muscles in normal human subjects. In *New Developments in Electromyography and Clinical Neurophysiology*, vol. 3, ed. DESMEDT, J. E., pp. 251–262. Basel: Karger.

VALLBO, Å. B. (1974*a*). Afferent discharge from human muscle spindles in non-contracting muscles. Steady state impulse frequency as a function of joint angle. *Acta physiol. scand.* **90**, 303–318.

VALLBO, Å. B. (1974*b*). Human muscle spindle discharge during isometric voluntary contractions. Amplitude relation between spindle frequency and torque. *Acta physiol. scand.* **90**, 319–336.