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THE PROJECTION OF JAW ELEVATOR MUSCLE SPINDLE AFFERENTS TO FIFTH NERVE MOTONEURONES IN THE CAT

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SUMMARY

1. By spike-triggered averaging of intracellular synaptic noise it has been shown in pentobarbitone anaesthetized cats that jaw elevator muscle spindle afferents with their cell bodies in the mid-brain have a relatively weak monosynaptic projection to masseter and temporalis motoneurones.

2. Extending the spike-triggered averaging method to recording extracellular excitatory field potentials it has been shown that virtually all the spindles do project monosynaptically to the motoneurone pool. It is concluded that the general weakness of the projection is due to its restriction to a small proportion of the motoneurones, possibly those concerned most with tonic postural functions.

3. The shape of individual intracellular e.p.s.p.s together with the spatial distribution of extracellular excitatory potential fields provide some evidence for a dentrically weighted distribution of the synapses.

4. Evidence is presented that both primary- and secondary-type spindle afferents project monosynaptically, the secondary effects being some 71 % of the strength of the primary ones.

INTRODUCTION

Observations made during normal masticatory movements in cats have shown two classes of behaviour of jaw elevator muscle spindle afferents. One group, thought to be from primary endings, were maximally active during passive muscle lengthening, but were commonly silenced by shortening. The other, apparently from secondary endings, showed an approximately linear relationship of firing frequency to length during both phases (Taylor & Cody, 1974; Cody, Harrison & Taylor, 1975). Understanding the use to which this sensory inflow is put during normal movements depends on a knowledge of the central connexions of the spindles, which is at present very incomplete. An additional reason for studying the details of jaw elevator spindle projection is that the jaw stretch reflex has some features of contrast with that of the hind limb. The afferent and efferent fibres pass in a special trunk, the portio minor of the fifth nerve (Szentagothai, 1948; McIntyre, 1951) and the first-order afferent cell bodies lie not in the trigeminal ganglion but within the mid-brain (Cajal, 1909) in association with similar cells from periodontal receptors (Corbin &

Harrison, 1940; Jerge, 1963; Cody, Harrison, Taylor & Weghofer, 1974). In this paper we examine their projection to the jaw elevator motoneurones, to see whether the connexions of the jaw-elevator secondary endings as well as the primaries are excitatory and monosynaptic, as recently shown to be the case for cat intercostal and triceps surae muscles (Kirkwood & Sears, 1974, 1975; Stauffer, Watt, Taylor, Reinking & Stuart, 1976) and to estimate their strength and other properties.

The classical methods of graded electrical stimulation for separately exciting different afferent modalities are not generally applicable in the cranial nerve situation because there is no evidence that afferent modalities are restricted to particular parts of the fibre diameter spectrum. The alternative, introduced by Mendell & Henneman (1968), is the 'spike triggered avarage' method by which intracellularly recorded synaptic noise is cross-correlated with the firing of a single physiologically characterized afferent. In the case of the jaw muscles this is especially attractive since the relevant first-order cell bodies located in the mesencephalic nucleus of the fifth nerve (MeV) are readily accessible to single unit recording by extracellular metal micro-electrodes. We use this technique here and an extension of it for recording extracellular fields within the motor nucleus (MotV) due to single afferents whose cell bodies are located in the MeV. Both primary and secondary afferents are shown to make monosynaptic connexions, but in a more restricted fashion than in the spinal cord and with a greater tendency to dendritic rather than somatic location on jaw elevator motoneurones.

METHODS

Cats were used of either sex in the weight range 2·5–4 kg. They were anaesthetized with I.P. sodium pentobarbitone (40 mg/kg) supplemented by I.V. doses of 12–24 mg. Penicillin and streptomycin (Crystamycin 0·2 ml. I.M.) were given at the beginning and 5% glucose in 0·4% saline I.V. at intervals. Succinyl choline was given in doses of 200 μg/kg to enhance the dynamic sensitivity of spindle primary endings, and some animals received gallamine triethiodide (20 mg) to eliminate disturbance from the electromyogram (e.m.g.) when recording central fields in response to stimulation of intact muscle nerves.

Stimulating electrodes were placed around masseter nerve on one side in all cases, and when possible around part of temporalis nerve. The nerves were exposed by removing the zygoma and parting the muscles. The electrodes consisted of pairs of enamelled silver wires cemented to a screw in the bone. They were manipulated into position and made rigid with acrylic cement. Fascia and skin were closed over the electrodes. Pairs of enamelled silver wires with their terminal 10 mm bared were inserted into each of the muscles, masseter, temporalis, pterygoid and anterior digastric for e.m.g. recording. Arterial, venous and tracheal canulae and a bladder catheter were inserted, and arterial blood pressure and rectal temperature monitored.

The animal was transferred to a stereotaxic head holder (La Précision Cinématographique) and two holes made in the skull: one for an electrode at 30° in front of the vertical, aimed at the MeV, and the other at 30° behind the vertical aimed at the fifth nerve motor nucleus (MotV). In each case the dura was incised and reflected and an oil-filled skin pool formed. For stretching the jaw elevator muscles a length-servo-controlled vibrator was attached to a screw driven into the symphysis menti.

Muscle spindle afferents in the MeV were located by advancing a glass-coated tungsten micro-electrode (Merrill & Ainsworth, 1972) in a plane 2·5 mm lateral while rhythmically moving the mandible, generally starting to explore near the middle of the superior colliculus. Units were then identified and characterized according to their muscle of origin by probing and jaw movement and sometimes by stimulating the masseter or temporalis nerve (see Cody, Lee & Taylor, 1962). They were also classified according to their dynamic index to ramp stretch (Crowe & Matthews, 1964; Cody *et al.* 1972) using a ramp of 4·5°/sec for 1·5° starting from approximately 10° of jaw opening.

Intracellular recording in the MotV was achieved with pipettes made from 1·5 mm diameter glass, pressure-filled with 0·8 M-potassium sulphate or citrate and bevelled to have a resistance of 3–10 MΩ. These could penetrate intact through the whole cerebellum in a proportion of cases. The motor nucleus is a small target ($\approx$ 1 mm diameter) and deeply situated, making it difficult to locate stereotaxically. Antidromically excited extracellular fields could reach 2 mV within the nucleus, but as little as 0·5 mm distant were small and unhelpful in indicating which way to move the electrodes. It was therefore found very convenient to explore the nucleus first with a tungsten electrode (50–100 μm tip exposed) used for stimulation with pulses of 0·1 msec, 1 per sec, 5 V, while monitoring e.m.g. responses in the various muscles. When a point of low threshold (0·2–0·5 V with electrodes of 1 MΩ impedance at 50 Hz) had been found, the electrode could be switched to record antidromic fields. With the nucleus thus located, the electrode could be changed for a pipette aimed as nearly as possible at the same point.

For recording within the motor nucleus both from pipettes and tungsten electrodes, a DC electrometer (W.P.I. M4) was used and its output displayed on one channel at 20 mV/cm DC–10 kHz and on another at 100 μV/cm, 1·6 Hz to 3·2 kHz. The recording system was a four-channel fibre-optics recorder (Medelec MS6) with digital delay line (SD6) and digital averager (DAV6) modified to receive sweep trigger pulses derived from the sensory spikes in MeV while averaging the high-gain AC records from MotV. The delay line permitted a 3 msec period before the trigger to be averaged which is particularly useful for establishing a control base line. The sampling rate was 34 kHz with 8-bit precision using 1024 samples for 30 msec, and displaying with 8-point linear interpolation. Most often 1024 sweeps were summated for STA. All records, both intracellular and extracellular, are shown with positive upwards.

RESULTS

Individual e.p.s.p.s

Intracellular averaging from jaw elevator motoneurones with the trigger signal derived from spindle afferents in the MeV yielded a number of depolarizing responses resembling small e.p.s.p.s as seen previously by this technique in the spinal cord (Mendell & Henneman, 1971). Examples are shown in Fig. 1. Their amplitude ranged from 3·1 to 60 μV (mean 18·3 S.D. 15·4, n = 14). The latency of these 'individual' e.p.s.p.s from the firing of the first-order cell body in the MeV ranged from $-0{\cdot}2$ to $+0{\cdot}9$ msec measured from the positive peak of the extracellular spike (mean 0·24 S.D. 0·30 msec), thus in some cases actually preceding the trigger. The explanation for this is evident from the diagram in Fig. 5 inset. An action potential arriving from the spindle afferent will spread into the two branches; one to the motoneurone pool the other to the sensory nucleus. The observed latency will then depend on the difference in the time taken to arrive at the MeV and to generate a soma spike on the one hand and to propagate to the MotV and to cross a synapse on the other. The mean latency of 0·24 msec means that, allowing 0·4 msec for synaptic delay (as found most commonly for spindle afferents to motoneurones in the lumbar spinal cord by Watt, Stauffer, Taylor, Reinking & Stuart, 1976) only some 0·16 msec exists for average conduction difference between the two axon branches. The question of latency will be dealt with further below, but meanwhile it seems very probable that these individual e.p.s.p.s are the result of a monosynaptic connexion.

The small sample size reflects both the difficulty of retaining stable recording simultaneously with both intra- and extracellular electrodes and the fact that individual e.p.s.p.s were only detectable in a proportion of otherwise acceptable recording situations. Thus, out of ninety-one recordings in fifteen animals, only fourteen unequivocal e.p.s.p.s were observed. Taken at its face value this indicates a weak projection of spindles to motoneurones, both in respect of the number of

spindles projecting to any one motoneurone and of the size of individual e.p.s.p.s. In these same experiments the compound e.p.s.p.s generated in masseter motoneurones by stimulation of masseter nerve, just below the threshold for antidromic motor stimulation, were quite small (mean 1·04 mV, range 0·2–3 mV, $n = 7$). It is particularly interesting that when studying the unit homonymous projection of individual masseter spindles to masseter motoneurones, an e.p.s.p. was seen in only two out of eighteen appropriate recording situations, yet consistently in those cases tried these motoneurones had definite though small masseter nerve evoked e.p.s.p.s (mean 0·72 mV, range 0·2–2 mV, $n = 6$, two cats).

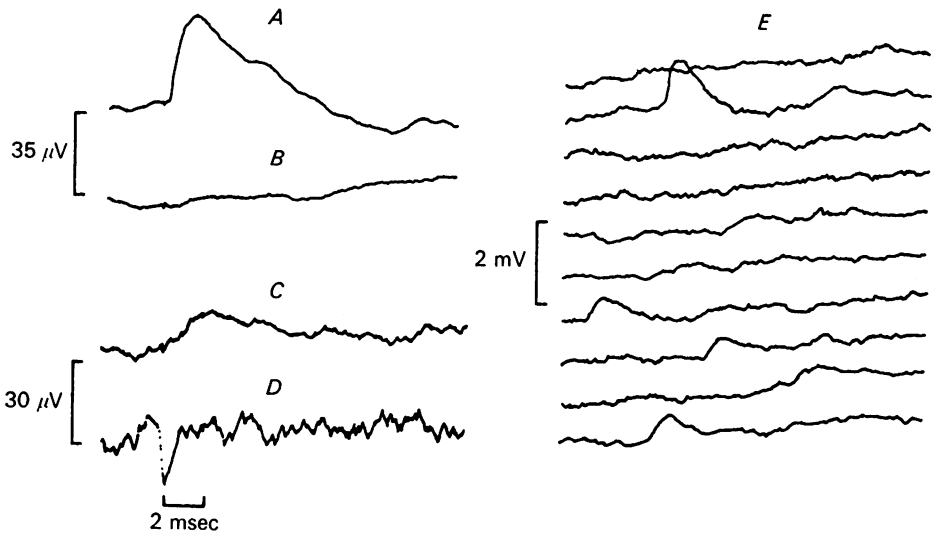

Fig. 1. Individual e.p.s.p.s recorded in jaw elevator motoneurones. *A*: average e.p.s.p. in masseter motoneurone, 1024 sweeps triggered from masseter spindle (static type). *B*: extracellular control, identical conditions. *C*: average e.p.s.p. in another elevator motoneurone, 1024 sweeps triggered from temporalis spindle. *D*: extracellular control, identical conditions. The moment of triggering by the cell spike in the MeV is indicated by the start of the 2 msec time bar. *E*: synaptic activity recorded in same motoneurone as in *C*, in response to jaw opening. Note voltage calibration.

Small individual e.p.s.p.s might be expected if synapses were dendritically located. The theoretical model of Rall (1967) offers a means of inferring the location of synapses on the basis of the relationship between rise time and duration above half amplitude. As can be seen from Fig. 2, points relating to ten reliably measurable e.p.s.p.s lie close to the theoretical line and seven have a shape appropriate to synaptic input beyond compartment 3. Data for the Ia input to lumbar motoneurones (Mendell & Henneman, 1971, Fig. 9) suggest spindle input to be approximately equally distributed to either side of the third compartment.

Despite the fact that STA e.p.s.p.s were relatively uncommon, on-going synaptic activity in motoneurones was usually enhanced by stretching the jaw elevator muscles. Often, large unitary e.p.s.p.s appeared (see Fig. 1*E*) of the order of 0·3–2·5 mV as previously noted in cord motoneurones (Burke & Nelson, 1966), far in excess of the size ever recorded by afferent unit triggered averaging. The possibility

should be considered that these originate from interneurones driven by spindle input. It should be noted that in the present work (unlike that of Watt *et al.* (1976) and Stauffer *et al.* (1976)) it is most unlikely that disynaptic connexions could be revealed by the STA method, because the anaesthesia used here was such as to reduce the responsiveness of the interneurones.

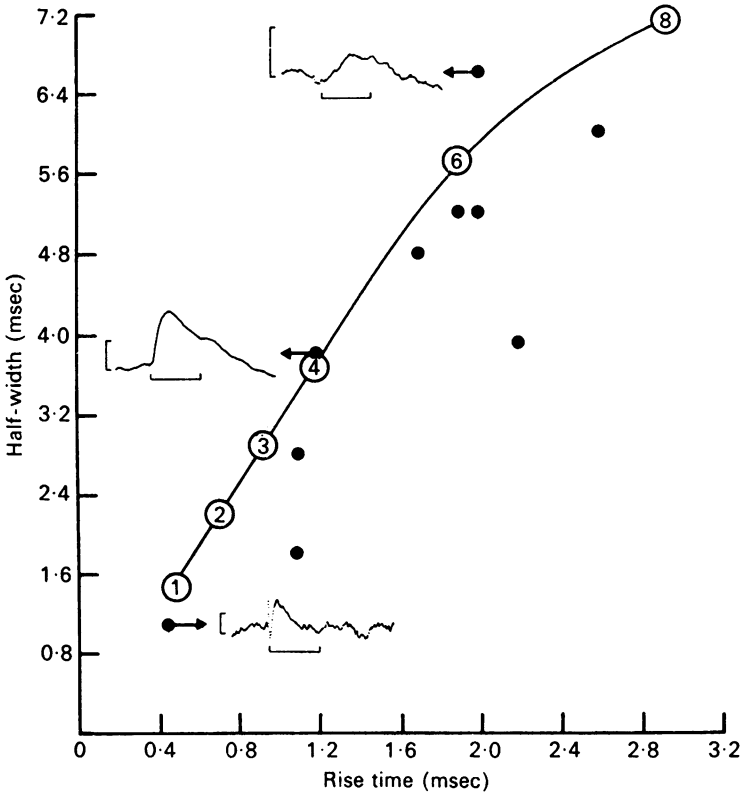

Fig. 2. Plot of half-width against rise time for ten averaged individual e.p.s.p.s (filled circles) recorded in jaw elevator motoneurones triggering from spindle afferents in the MeV. Three examples are inset against their data points. Calibrations: voltage 20 μV, time 4 msec. The theoretical curve is plotted from Rall (1967) with numbers to indicate successive compartments from soma to distal dendrites (medium duration current transient).

Extracellular fields due to single spindle afferents

It has previously been noted that a small extracellular negative field potential can be detected by averaging within a motoneurone pool when triggering from a single afferent. No special use has previously been made of such unit fields, they have merely been noted when extracellular records have been used as controls for intracellular averages. When recorded with micropipettes they were found to vary irregularly over very short distances (Watt *et al.* 1976). We have recently shown (Taylor, Stephens, Somjen, Appenteng & O'Donovan, 1977; Appenteng, O'Donovan, Somjen, Stephens & Taylor, 1977) that these unit extracellular fields are much better defined spatially when using a metal micro-electrode with a relatively large

tip exposed (50–100 μm). The larger lead-off area apparently bridges the short-range inhomogeneities which cause the variability of pipette recordings. Fig. 3 shows a typical record thus obtained from averaging within the motor nucleus while triggering from a jaw elevator spindle (the electrode track was initially adjusted to pass through the point of maximum negative antidromic field potential evoked by masseter-nerve stimulation). On tracking through the nucleus, a very distinct

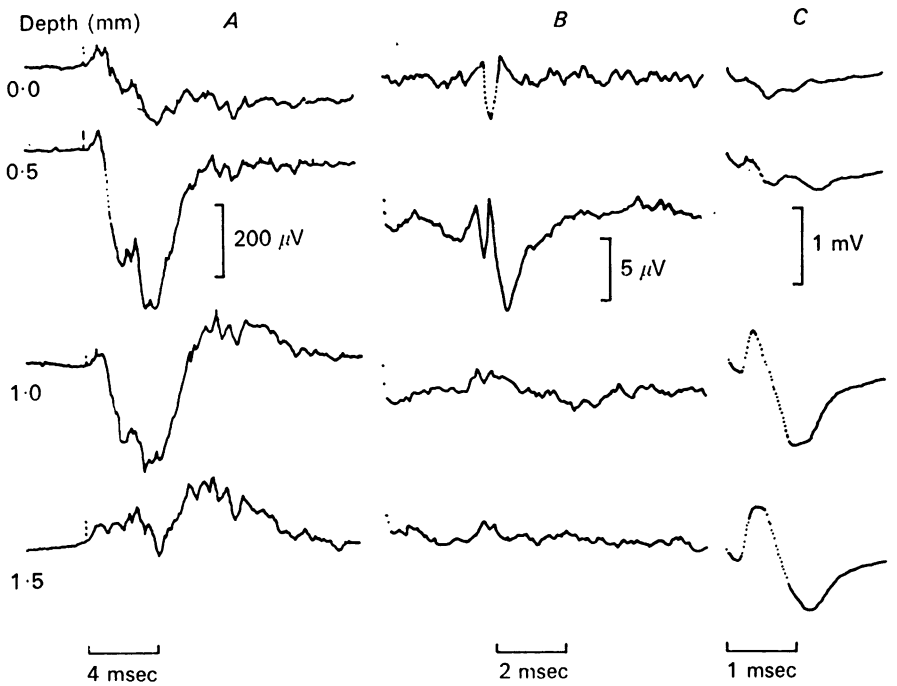

Fig. 3. Extracellular potential fields recorded on a track through the MotV at the depths indicated relative to an arbitrary zero dorsal to the nucleus. *A*: excitatory synaptic fields due to minute quick stretch of jaw elevators (averages of eight sweeps). *B*: STA field due to spindle in masseter (phasic type). Average of 1024 sweeps. *C*: responses to maximal temporalis nerve stimulation (averages of eight sweeps).

field was found at depths 0·5 mm below an arbitrary zero; 0·5 mm deeper the field was reversed and thereafter died away. Maximum negative response is to be expected with the electrode tip closest to the effective centre of the excitatory current sink, which must therefore be between depths 0 and 1·0 mm. Frequently, as in this example, a brief wavelet was seen with its initial (positive) peak preceding the negative field by a mean of 0·4 msec. It may be interpreted as due to spike propagation in presynaptic axon branches (see Jankowska & Roberts, 1972; Watt *et al.* 1976) and we refer to it as a presynaptic spike. Such spikes could often be detected immediately dorsal to the point at which a negative field could be seen but always disappeared as the nucleus was traversed to the region where the unit field reversed.

Extent of single afferent projection

The anatomical extent of the spindle excitatory projection has been studied by making systematic electrode tracks spaced at 0·5 mm intervals in a sagittal plane through the MotV, and recording at every 0·5 mm the fields due to (*A*) a quick stretch of the jaw elevators, (*B*) to a single afferent and (*C*) to muscle nerve stimulation. Examples of such fields from one experiment are shown in Fig. 3 while Fig. 4 shows

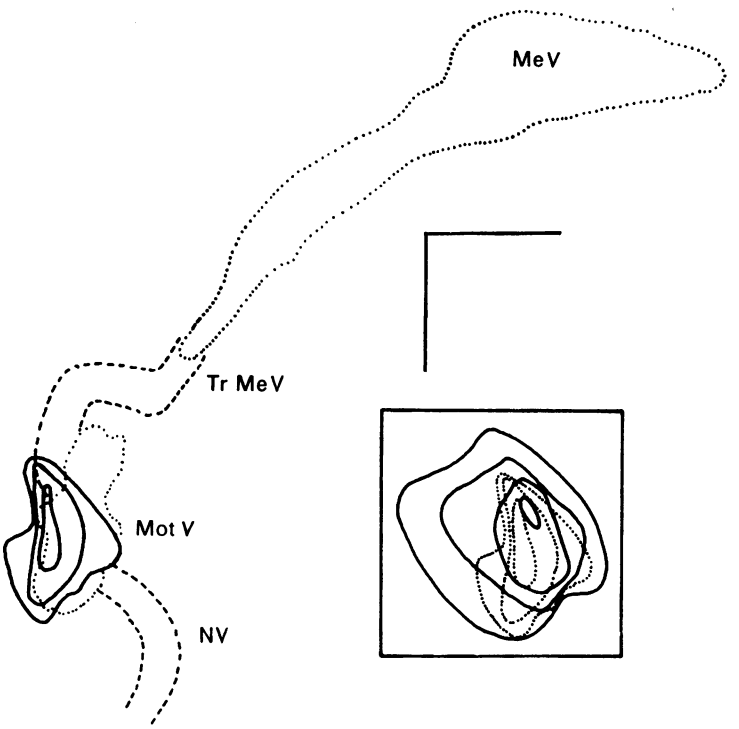

Fig. 4. Isopotential contour plots superimposed on diagram of MotV and MeV and related structures, projected on the sagittal plane. In the main diagram, the continuous isopotential lines derive from spike triggered averaging from a temporalis spindle. From without inwards they represent 0, $-0{\cdot}65\,\mu$V and $-4{\cdot}5\,\mu$V. In the inset, this plot shown dotted is overlayed by isopotential curves due to minute quick stretches having values of 0, $-125\,\mu$V, $-300\,\mu$V and $-600\,\mu$V from without inwards. Scale bars each represent 2 mm, intersecting at Horsley-Clarke zero. Tr MeV = tract of mesencephalic nucleus of the fifth nerve; NV = mixed fifth nerve trunk.

plots from another experiment of isopotential contour lines superimposed on a tracing of a parasagittal projection of the MotV and associated structures. Quick stretch can be expected to excite a large proportion of the phasic spindles in the jaw elevator muscles, which it is presumed must conjointly project widely throughout the elevator motoneurone pool. Thus the quick stretch field should outline the anatomical extent of MotV, which it evidently does (continuous line in inset to Fig. 4). The anatomical arrangement seen in Fig. 4 suggests that the motor axons leave the MotV ventrally and this is confirmed by the localization of the early positive wave due to antidromic stimulation in the ventral part (Fig. 3*C*), this wave being due to the

arriving nerve volley. Histologically we have observed a tendency for the motoneurone dendrites to radiate dorsally, so that an electrode penetrating from dorsal to ventral would pass successively amongst dendrites, cell bodies and axons. This may explain the sequence of recordings seen in Fig. 3, in which a well-developed negative quick stretch field lies dorsal to the main negative antidromically evoked field. The latter is presumably due to invasion of cell bodies and the concentration of inward synaptic current due to quick stretch dorsal to this could indicate a weighting of spindle synpases towards the dendrites – a suggestion previously made on the basis of the shape of intracellularly recorded STA e.p.s.p.s. The unit field in Fig. 4 lies within the quick stretch field but shows some sign of displacement of its centre. On other occasions the unit field is even more restricted as shown in Fig. 3*A*, *B*. In this case it is interesting that the unit field reverses polarity from maximum negative to maximum positive between depths 0·5 and 1·0 mm while the quick stretch field continues negative to beyond depth 1·0 mm and reverses to maximum positive at depth 1·5 mm.

Thus it appears that the extracellular STA method can be spatially quite specific in locating an excitatory projection. It follows that to some degree this projection of some individual afferents is restricted to parts of the MotV rather than being diffusely spread throughout its extent.

It appears (see also Taylor *et al.* 1977) that the STA method applied to extracellular fields can be a useful supplement to the intracellular method for mapping the projection of single afferents, because (*a*) bias towards sampling from large motoneurones should be less than with intracellular work, (*b*) the general effect on many motoneurones is revealed, and (*c*) the effect of a series of single afferents may be examined quite rapidly. This advantage is exploited in the following section.

Comparison of projections of phasic and static spindle afferents

(*a*) *Latency.* Anatomical studies (Szentagothai, 1948) have shown that all the afferents from both annulo-spiral and flower-spray endings in jaw elevator muscles enter the medulla through the minor root of the fifth nerve and pass into the tract of the mesencephalic nucleus. At least some of these make monosynaptic connexion in MotV as judged by anatomical (Szentogothai, 1948) and physiological evidence (Hugelin & Bonvallet, 1956). This is supported for specifically identified single afferents in the present work, but a question of further interest is whether monosynaptic connexions exist for both primary and secondary spindle afferents.

The identification of the MeV cells as primary or secondary presents practical problems because consistent conduction velocity differences have not been established to exist in this situation. We have measured central latency from masseter nerve stimulation and dynamic sensitivity to stretch and in a series of thirty-nine units have found no significant correlation. We have therefore relied solely on dynamic sensitivity to ramp stretch after sensitization by succinyl choline (Cody *et al.* 1972) and using standard ramps (see Methods) have chosen a dynamic index of 50 impulses/sec as the dividing line separating 'phasic' units from 'static' units. Out of 117 spindle afferents sixty-two were characterized as static (thirty-one from temporalis, twenty-one from masseter and ten unidentified) and fifty-five as phasic (thirty from temporalis, sixteen from masseter, four from pterygoid and five

unidentified). Of these, ninety-five (81 %) yielded unequivocal extracellular excitatory fields. The mean latency for phasic units was 0·27 msec (S.D. 0·13 msec, $n = 42$, range 0·71–0·08) and for static units 0·35 msec (S.D. 0·18, $n = 53$, range 0·87–0·10). The distributions of latencies (Fig. 5) were very similar for the two groups except that the longest latencies were predominantly associated with the static units. This led to a difference in the means significant at the 2 % level.

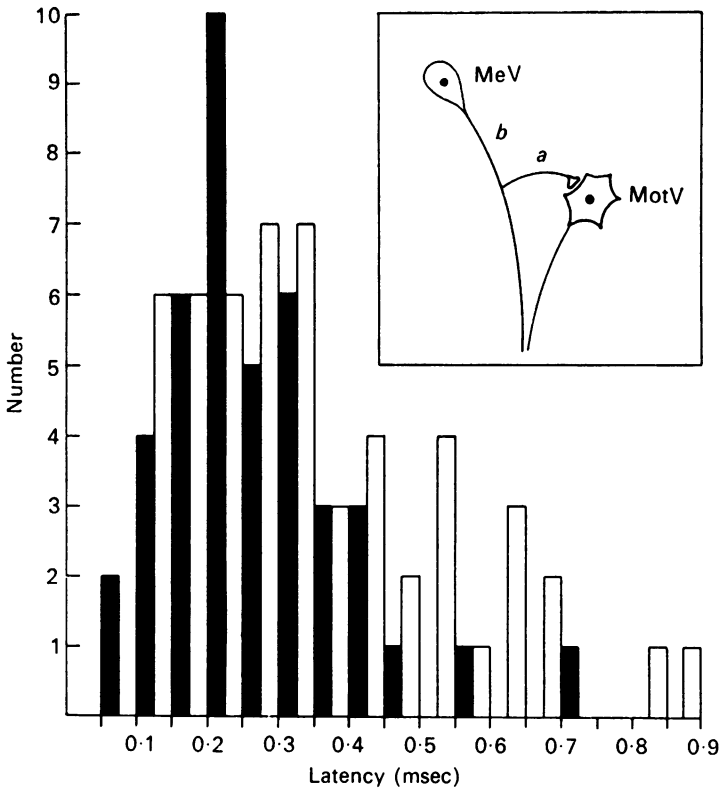

Fig. 5. Histogram of latencies of averaged extracellular field potentials within the MotV triggered from ninety-five different spindle afferents. Filled columns represent responses from phasic spindles, open columns from static spindles. Inset: diagram of branching of spindle afferent fibres on the way to cell body in MeV and to synaptic connexions in MotV. The segment labelled *a* is termed the collateral and *b* the unipolar process.

The interpretation of the latency is evident from Fig. 5 inset. Centripetal impulses invade the two branches, one to the cell body and the other to the terminals in the motor nucleus. If we take the conduction time for the collateral branch to MotV as *a* and for the unipolar process to MeV as *b*, then the observed latency of the extracellular field from a trigger spike in the MeV will be $a - b +$ time for synaptic transmission. Allowing 0·4 msec for synaptic delay (see Jankowska & Roberts, 1972; Watt *et al.* 1976) and taking 0·31 msec as the mean observed latency, $a - b = 0{\cdot}09$ msec. On two occasions it was possible to excite an MeV cell by stimulating via the tungsten electrode in the MotV with latencies of 0·52 and 0·56 msec. Taking a

mean value of 0·54 msec and allowing for an activation time of 0·2 msec (Jankowska & Roberts, 1972), $a+b$ = 0·34 msec. Consequently, conduction time (a) for branching point to terminals in MotV is estimated to be 0·12 msec and (b) for the branch to MeV 0·22 msec. Thus there is no time available for a second synapse and we must conclude that both phasic and tonic spindle afferents project monosynaptically. The value of $(a-b)$ may be estimated in two other ways. Stimulation of masseter nerve (Fig. 6A) evoked unit spikes in MeV with mean latency 1·17 msec (S.D. 0·41 msec, n = 39). Intracellular e.p.s.p.s in masseter motoneurones elicited by masseter nerve

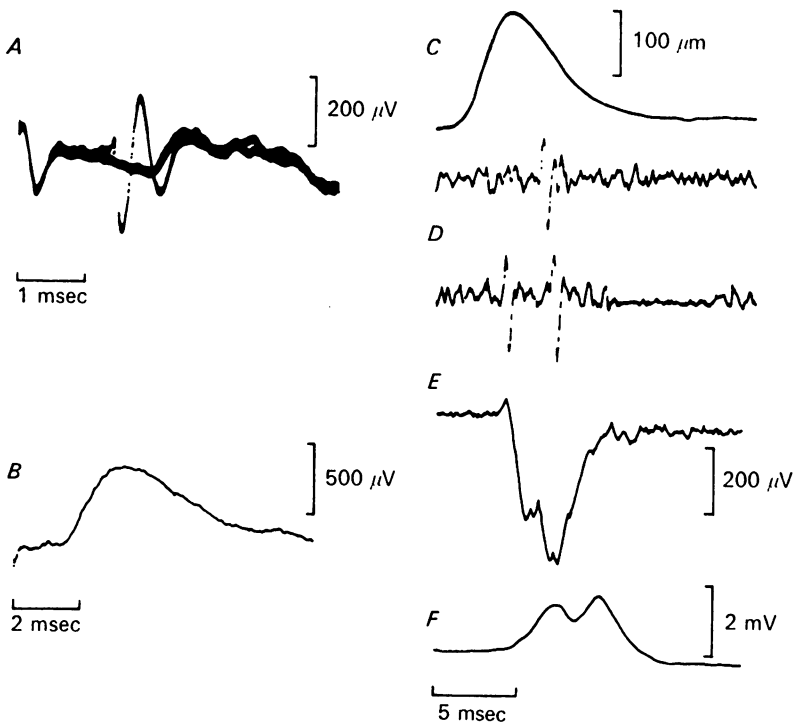

Fig. 6. A: all- or-none firing of cell in MeV when stimulating masseter nerve at threshold; five sweeps superimposed, two with unit firing. B: e.p.s.p. in elevator motoneurone in response to stimulation of masseter nerve at 1·2 × threshold. C: form of the minute quick stretch used to excite volley from jaw elevator spindles. D: two examples of firing of temporalis spindle cell in MeV in response to this transient stretch. E: example of excitatory synaptic extracellular field potential in MotV due to the same stretch evoked spindle volley. F: intracellular record from jaw elevator motoneurone to show timing of stretch evoked e.p.s.p.

stimulation (Fig. 6B) had mean latency 1·36 msec (n = 5). Again allowing 0·4 msec for a single synaptic delay we are left with an estimate for $a-b$ = 0·21 msec.

Very small transient muscle stretches are known to be rather specific in exciting spindle primaries (Lundberg & Winsbury, 1960; Stuart, Mosher, Gerlach & Reinking, 1970; Stuart, Willis & Reinking, 1971). In the present experiments, we have regularly used stretches of 50–150 μm amplitude and about 8 msec duration applied at the symphysis menti and have found these to produce 1 or 2 spikes in a proportion of spindle afferents in the MeV (Fig. 6C, D) and extracellular excitatory fields amongst

jaw elevator motoneurones (Fig. 6*C*). Mean latency of the first spikes was 3·25 msec and for extracellular fields was 3·4 msec, a difference of 0·15 and again allowing 0·4 msec for one synaptic delay, $a-b = -0{\cdot}25$ msec.

On the occasion when terminals were stimulated in the MotV and a latency found for MeV spikes of 0·54 msec the direct distance between the electrode tips was 3·9 mm. This gives an estimate for conduction velocity of $3{\cdot}9/(0{\cdot}54-0{\cdot}2) = 11{\cdot}5$ m/sec, a value not disimilar to that found for intra-cord velocities of Ia branches (Fu, Santini & Schomburg, 1974).

(*b*) *Strength.* The pooled data for all unitary field amplitudes recorded at their point of maximum gave a mean value of 3·65 μV (S.D. 2·49, $n = 115$). These unitary fields, convenient as they are for identifying the existence of a synaptic connexion, may not give a readily interpretable quantitative idea of the strength of the synaptic effect in the way that intracellular averaging does, but they can be used for comparative purposes. Thus, comparing unit fields for static and phasic, the mean amplitude for the former was 3·2 μV (S.D. 2·0 μV, $n = 53$) and for the latter 4·4 μV (S.D. 2·9 μV, $n = 43$), a significant difference ($P < 0{\cdot}02$), implying that phasic spindles have on average a stronger monosynaptic connexion that the static ones. The rise times of the negative unit fields were shortest when the electrode was positioned for maximum response amplitude. Measured at this point the mean value for static units was 0·80 msec (S.D. 0·56 msec, $n = 21$) and for phasic units 0·70 msec (S.D. 0·35 msec, $n = 17$). There was no significant difference.

Possible specialization in the MeV regarding projection to MotV

The classical histological studies of the MeV summarized by Cajal (1909) suggest the existence of some differences between the cells of the rostral and caudal parts of the nucleus. Coupled with this our recent finding that the first order cells of periodontal mechanoreceptors are concentrated in the caudal part (Cody *et al.* 1974) of the nucleus had raised the question as to whether there might be some specialization in the nature of the connexions from the two parts (Harrison, Somjen, Stephens & Taylor, 1976). We have tested this by comparing unit fields in the motor nucleus obtained by triggering from the different spindle afferents. So far, no quantitative differences have been observed in the frequency or strength of synaptic projection from the two parts.

Latencies of the unit excitatory fields were shorter when timed from rostral MeV cells than from caudal ones. In one experiment in which six cells from the middle of the nucleus were compared with six cells located 3·12 mm caudally, the mean field latencies differed by 0·15 msec. The explanation is clearly that the greater conduction distance to the rostral cells causes the trigger spike to occur later relative to the arrival of activity in collateral terminals in the MotV. The mean conduction velocity of the MeV cell processes is then estimated at 20·7 m/sec, which interestingly is faster than our estimate of 11·4 m/sec for the collateral and unipolar process together, implying that the collateral conducts the more slowly.

DISCUSSION

Questions posed at the beginning of this work were whether spindle secondaries, as well as primaries, made excitatory connexion to motoneurones of the jaw elevators and if so whether monosynaptically and how strongly. The practical problem of identification of spindle primaries and secondaries has been discussed. Accepting the identification, based on dynamic index after succinylcholine we are able to answer the first two questions, and say on the basis of the extracellular excitatory fields elicited by STA that both types of spindle afferents connect to give monosynaptic excitation. In point of fact no real problem arises due to uncertainties in identification because virtually all spindle afferent cells in the MeV appear to be so connected. With regard to the relative strengths of the monosynaptic projections, the presumed secondaries gave excitatory field potentials averaging 71% of the amplitude of those due to presumed primaries. We have no intracellular STA data to compare the primary and secondary projection strength, in terms of unit e.p.s.p. size, because the technical difficulty of those experiments precluded the additional complication of functionally typing the afferent. However, the present observations can be added to those of Kirkwood & Sears (1974, 1975) and of Stauffer *et al.* (1976) in showing the generality of autogenetic monosynaptic excitatory connexions from spindle secondaries. In the latter study on triceps surae, the intracellular Group II evoked unit e.p.s.p.s averaged 46% the amplitude of the Group Ia e.p.s.p.s.

The significance of the jaw-spindle monosynaptic projection will not be clear till we can establish its quantitative effectiveness in modulating the discharge of elevator motoneurones; however, the existence of a monosynaptic projection of the secondaries adds further interest to our earlier observations on spindle secondary behaviour during normal jaw movements (Taylor & Cody, 1974; Cody *et al.* 1975). The presumed secondaries fired throughout eating and lapping movements with a tolerably linear relation of firing frequency to length. We are led inevitably to the conclusion that these afferents have the essential characteristics required for negative feedback control of active muscle shortening, though the strength of feed-back at least by the monosynaptic path seems to be very modest.

We were surprised to find that only a small proportion of the jaw elevator motoneurones displayed individual e.p.s.p.s when triggering from muscle spindle afferents even when studying the homonymous projection. At first we were concerned that anaesthesia or deterioration of the preparation may have been important; however, this did not appear to be the case because substantial extracellular excitatory fields within MotV were always elicitable by quick stretch evoked spindle primary volleys, and most motoneurones penetrated displayed plentiful ongoing synaptic activity from other sources. Furthermore, motoneurones in which no individual e.p.s.p.s could be detected by STA from particular spindle afferents did show small but unequivocal e.p.s.p.s on muscle nerve stimulation. We are led then to the conclusion that individual jaw elevator motoneurones receive a monosynaptic projection from only a small proportion of the related spindle afferents. All such afferents appear to project to the motoneurone pool because all were found to produce appreciable excitatory fields at some point within the nucleus, but each projects to only a limited selection of the motoneurones. This contrasts with the hind-limb extensor situation

where it is now well known (Mendell & Henneman, 1971; Watt *et al.* 1976) that individual spindles project very widely within the pools and influence nearly all homonymous and a large proportion of heteronymous motoneurones.

Two factors could help to explain a more selective spindle projection here than in the hind-limb extensors. First, it is clear that mechanically the jaw elevators are not simple muscles with single points of insertion like many of the hind-limb muscles. Therefore it may not be appropriate for spindles from one part of the jaw muscles to project diffusely throughout the motoneurone pool, but rather to be restricted to motoneurones with mechanically similar actions. Secondly, the jaw elevators in the cat are predominantly composed of fast twitch muscle fibres (Taylor, Cody & Bosley, 1973). The units activated in tonic stretch reflexes are limited to small portions in the anterior part of temporalis (see also Møller, 1976) and are found to be small and relatively slow in their contraction characteristics (Taylor, 1976). Such units, with low threshold and tonic behaviour, are likely to have small motoneurones (Burke, 1968*a*) which, being more difficult to impale than large ones, will seem unduly rare. If the specialization of small slow motor units with relatively strong monosynaptic Ia projection and a propensity for tonic firing (Burke, 1968*a*, *b*) seen in the triceps surae can be connected with postural function then it would not be unexpected that such units should be a much smaller proportion of the whole in the jaw elevator. The force needed to support the jaw must be a much smaller proportion of total contraction strength of the jaw closers than the force needed to support the body is of the strength of the hind-limb extensors. An interesting extension of the present work would be to correlate mechanical properties of jaw motor units obtained by intracellular stimulation (Burke, 1967) with the size of unit e.p.s.p.s from spindle afferents obtained by STA of intracellular synaptic potentials. If it could be confirmed in the case of the jaw elevators that the rarity of motoneurones showing monosynaptic unit e.p.s.p.s is because these occur principally in the minority motoneurones used in tonic postural activity it would begin to appear that the significance of the monosynaptic projection might be related to its suitability for relatively inflexible or constant requirements of postural control. We might then have to look much more seriously at multisynaptic rather than monosynaptic excitatory connexions of spindles as the basis for load compensation or servo action (see Matthews, 1972, pp. 357–361). Multisynaptic pathways would in any case be well adapted for this purpose, because the necessary flexibility of control could be achieved by rapid switching of interneurones by descending influences.

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