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A FUNCTIONAL ANALYSIS OF THE COMPONENTS OF THE MESENCEPHALIC NUCLEUS OF THE FIFTH NERVE IN THE CAT

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SUMMARY

1. The mesencephalic nucleus of the trigeminal nerve has been studied using extracellular micro-electrode recording and the constituent cell types identified.

2. Two types of unit were found, namely, muscle spindle first order afferents of ipsilateral jaw-closing muscles and mechanoreceptor afferents of ipsilateral maxillary and mandibular teeth.

3. No evidence was found for representation of extra-ocular muscle stretch receptors, of temporo-mandibular joint receptors or of tendon organs of jaw muscles.

4. Spindle units of each of the jaw-closing muscles were recorded in all parts of the nucleus and there was no evidence of their segregation according to muscle of origin.

5. Attempts to classify spindle units by their dynamic response to ramp stretches, their following of high frequency vibration and their interspike interval variability at constant length gave no indication of two populations when fusimotor activity was suppressed.

6. Following the injection of suxamethonium, however, units fell into two groups according to their dynamic index. Their behaviour resembled that described for primary and secondary spindle afferents. In data pooled from all of the jaw-closing muscles there were approximately equal numbers of units in each group.

INTRODUCTION

Much of our knowledge of muscle spindles comes from studies of the hind-limb muscles of the cat, which have contraction speeds (time to peak twitch) of 27–70 msec (Buller, Eccles & Eccles, 1960). One of the purposes

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of the present work was to examine the properties of spindles in the very fast jaw-closing muscles, which are known to be able to reach peak twitch tension in 11 msec (Taylor & Davey, 1968).

The mesencephalic nucleus of the fifth cranial nerve (MeNV) is a collection of cells morphologically similar to dorsal root ganglion cells and believed to be primary or first order neurones from proprioceptors in the cranial region (Cajal, 1909; Hosokawa, 1961). In particular, muscle spindle afferents of the jaw-closing muscles (masseter, temporalis and pterygoid) appear to be represented and are accessible to extracellular micro-electrode recording (Jerge, 1963). Sampling spindle afferents by this means is perhaps less likely to be biased according to fibre diameter than in the case of dorsal root filament recording. This is important in determining whether primary and secondary afferents form two distinct groups separable by physiological means, or are a single continuous population. Evidence for such a division has been presented for the hind-limb muscles (Matthews, 1963), but classification has been unsuccessful in other situations (Koeze, 1968; Bach-y-Rita & Ito, 1966).

In addition, it was hoped to resolve some inconsistencies in the findings of previous workers concerning the cell types present in the MeNV. The original physiological observations on the nucleus and its root (Pfaffman, 1939; Corbin & Harrison, 1940) indicated that units associated with spindles of the masticatory muscles and periodontal receptors were represented, and this has been confirmed (Jerge, 1963; Taylor & Davey, 1968; Cody, Lee & Taylor, 1972). Smith (1969) claimed that tendon organ cell bodies were also present, though the evidence of Szentagothai (1948) is against this and suggests their presence in the trigeminal ganglion. Much uncertainty also surrounds the question of the location of eye muscle proprioceptor first order cells (Hosokawa, 1961; Whitteridge, 1960). A widely held view is that they also are present in the MeNV (Cooper & Fillenz, 1955; Fillenz, 1955). On the other hand, evidence from the pig and sheep (Manni, Bortolami & Desole, 1966, 1968) places them in the trigeminal ganglion. Recordings from more than five hundred single units in the nucleus have permitted us to check some of these possibilities in the cat.

METHODS

Adult cats, male and female, in the weight range 2–3 kg were used. They were anaesthetized with sodium pentobarbitone (60 mg/kg I.P.) and maintained at a deep level by I.V. supplements. In later experiments, while recording from muscle spindles, chlorpromazine (I.V. doses of 5 mg half hourly) was used in addition to suppress fusimotor activity. Such doses of chlorpromazine are greater than those shown by Henatsch & Ingvar (1956) to abolish spontaneous and reflexly evoked fusimotor discharge, particularly in combination with pentobarbitone which Voorhoeve & van Kanten (1962) have shown to have similar, though less specific, action.

The animal's head was held in a stereotaxic device (La Précision Cinématographique, for visual experiments) and electrodes inserted vertically through a hole in the cranium, usually with the superior colliculus exposed by hemispherectomy. Access to the more caudal regions of the MeNV was provided by drilling away part of the tentorium.

Recording. Glass-coated tungsten micro-electrodes (Merrill & Ainsworth, 1972) were used, with impedance 1–3 MΩ at 1·7 kHz. Action potentials triggered an instantaneous frequency display circuit.

The whole extent of the MeNV, as determined by histology, was explored. The region of interest is a rostro-caudal strip approximately 1 mm wide and 8 mm in length, centred on the mid-point of the superior colliculus and 2·3 mm from the midline. Electrode tracks were generally spaced at 200 μ intervals. Thirty-nine animals were used and the total number of electrode tracks was seven hundred and seventy-nine.

Application of muscle stretch. The mandible was secured to a light V-shaped frame pivoted about an axis through the temporo-mandibular joints. The apex of the V was coupled to an electromagnetic displacement servo (Pye–Ling V 50 vibrator). The stimuli were ramps of 1·5 degrees of jaw opening starting from 8·5 degrees at velocities of 1·0, 2·2, 3·25, 4·5 and 10·0°/sec. Small amplitude vibrations were also applied at increasing frequencies up to 300 Hz. The maximum frequency at which a receptor could reliably give one impulse per cycle is referred to as the following frequency. Stretch of extra-ocular muscles was produced by passive rotation of the eyeball using a suction cup and stem.

Stimulation of muscles. Pairs of enamelled wires with their final 2 mm bared were inserted into each of the jaw-closing muscles. The pterygoid was reached through the palate.

Histology. In many cases the animals were perfused after death with saline followed by formol saline and the brains subsequently examined for the location of the electrode tracks. Detailed histological studies will be reported elsewhere.

RESULTS

During the exploration of the mid-brain, ramp stretches were continuously applied to the jaw with a cycle period of 2 sec. When the region of the dorsolateral aspect of the central grey matter was approached unitary activity was detected in time with opening movement. Thereafter as the electrode was advanced to isolate a single unit, tests for tooth receptors and eye muscle receptors were frequently applied, together with occasional testing for other sensory input from the head. The only activity detected in this region, in these deeply anaesthetized animals, was related to jaw opening or to tooth pressure. Occasionally, a unit was encountered which was sensitive to eye movement, but invariably it proved not to be specific to direction of rotation. Also, such units were more affected by eyeball pressure (which would relax most of the extrinsic eye muscles) than by traction. They were always, in addition, extremely sensitive to jaw opening and to local pressure on particular jaw muscles. In recording from more than 500 units, we have never found one specifically related to eye movement.

Cells responding to pressure on teeth were encountered, as described by Jerge (1963). They were most commonly associated with mandibular or maxillary canines. Some were quite specific with regard to direction of pressure on a single tooth, while others could be excited by pressure on several teeth or surrounding gum. They were less plentiful than units responding to jaw opening, but showed no sign of being specifically segregated from them. No further attention was directed to these tooth receptors.

Turning to the cells related to jaw movement, they were always excited by jaw opening, never by closing. They could therefore only have been connected with stretch receptors in the jaw-closing muscles (temporalis, masseter, pterygoid) or possibly with temporo-mandibular joint receptors. The latter possibility is unlikely in view of their unidirectional sensitivity. Furthermore, they could always be activated by light local pressure on one or other of the above three muscles, with the jaw held still. In all cases, the possibility of joint receptors was eliminated in these ways and by the more specific positive tests for muscle spindles, described below.

Before proceeding to analyse the functional characteristics of the muscle stretch receptors, it is worth considering the evidence for the cells concerned being first order. The cells regarded as constituting the MeNV (Cajal, 1909) are large unipolar cells scattered thinly over the dorsolateral surface of the central grey. They are morphologically very similar to dorsal root ganglion cells and show chromatolysis on cutting the root of the fifth nerve (May & Horsley, 1910). Our recordings were always from the region in which these cells were to be found histologically. The unitary activity was very resistant to anaesthesia and could persist for some minutes after respiration had been arrested with pentobarbitone. It was also notable that the cells very seldom showed signs of injury by repeated close passage of the electrode tip. This is consistent with the cells having no dendritic tree. In those few cases in which other, unrelated, activity was noticed in this region, the jaw-opening units generally gave larger extracellular action potentials, as expected from the large size of first order somata in the MeNV. Latency measurements were not attempted in these experiments because of the difficulty of exposing the relevant nerves without destroying large parts of the muscles, and because the conduction distances are so uncertain.

Distinction of cells belonging to muscle spindles and tendon organs

On the basis of their responses to muscle twitches, most of the jaw-closing muscle stretch receptors could be immediately classified as belonging to muscle spindles. Some typical records are shown in Fig. 1. The large artifacts at the beginning of the records due to synchronous muscle

action potential could not be avoided, but they do not obscure the spindle type responses of the units, i.e. cessation of discharge during the rising phase and a burst during the falling phase of contraction. Occasionally, contraction of one of the jaw muscles resulted in a discharge during the rising phase of the twitch, suggesting a tendon organ in that muscle.

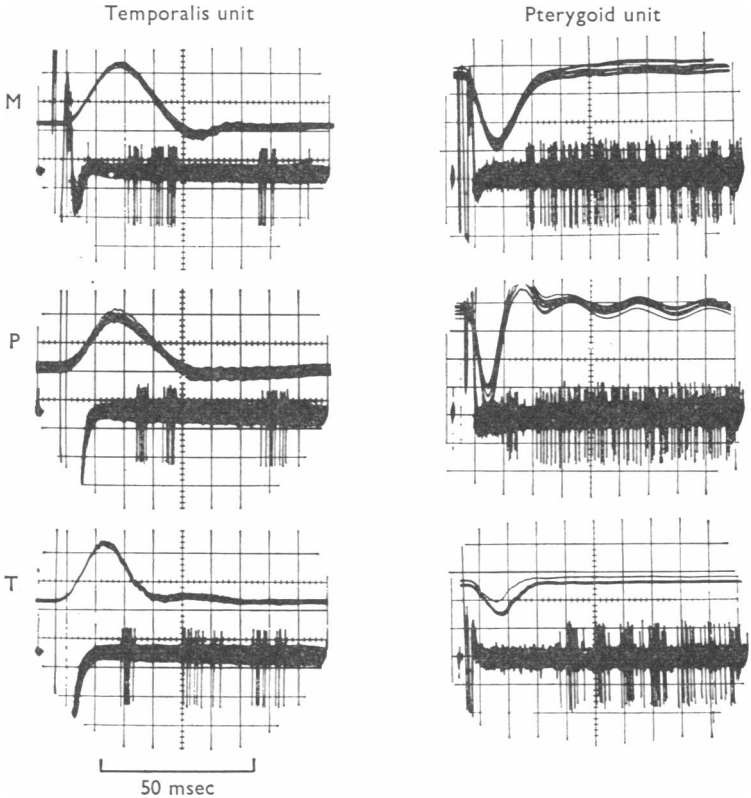

Fig. 1. Responses of two units in the MeNV to twitches of masseter (M), pterygoid (P) and temporalis (T). In each case ten responses are superimposed. The upper trace represents displacement of the jaw. Jaw closing is upward for the temporalis unit (left) and downward for the pterygoid unit (right).

However, closer examination always revealed that the muscle being stimulated was not that in which the receptor was located. The true muscle of origin of the afferent was being stretched by the twitch in its neighbour. Although the three muscles are essentially in parallel as regards jaw opening and closing movements, they can have opposing effects in lateral sliding motion at the temporo-mandibular joint. For example, contraction of masseter not only closes the jaw, but also deflects it laterally and can

stretch pterygoid. In the work reported by Taylor & Davey (1968), in which tendon organ cell bodies were believed to be occasionally found, the problems of this mechanical situation had not been fully appreciated. Study of many more units has now made it clear that all the jaw movement sensitive cells in the MeNV can be accounted for as belonging to spindles in jaw-closing muscles. This was supported by the response of a limited number of units tested with intra-carotid arterial, and of a larger number to I.V. injection of suxamethonium (SCh). Activation was consistently produced, a characteristic of spindle afferents not found with tendon

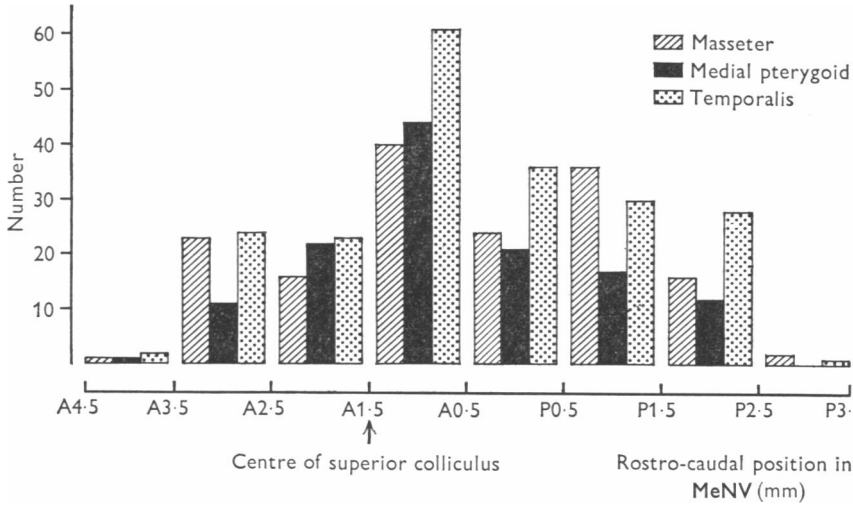

Fig. 2. Distribution of spindle units in the MeNV according to their muscle of origin. The abscissa is graduated in mm of rostro-caudal displacement from the ear-bar zero.

organs (Granit, Skoglund & Thesleff, 1953). In addition, in a number of preliminary experiments jaw-opening units were examined in lightly anaesthetized cats. Under these conditions such units always showed conspicuous frequency changes with pinna twisting (Granit, Job & Kaada, 1952).

Distribution of spindle units according to muscle of origin

The muscle of origin of cell bodies of spindle afferents was identified by (*a*) application of surface pressure to each muscle, (*b*) electrical stimulation of each muscle, (*c*) manipulation of the mandible and (*d*) pressure on the eyeball. Muscle pressure normally allowed reasonably certain localization, one muscle being much more sensitive to probing than the others. In addition, lateral deflexion of the jaw preferentially stretches pterygoid and medial deflexion stretches masseter, and to a lesser extent, temporalis.

Units from each of the jaw-closing muscles were found in all regions of the nucleus (Fig. 2). Applying the χ^2 test, no differences in relative distribution of units from the three muscles could be detected. No attempt was made to examine the medio-lateral distribution because of the narrowness of the nucleus.

Classification of spindle units

Attempts were made to distinguish primary and secondary spindle afferents by the following tests: (*a*) dynamic index (DI) of Crowe & Matthews (1964). Jaw opening was of amplitude 1·5° from 8·5° of opening at velocities 1·0, 2·2, 3·25 and 4·5°/sec. A quotient was also

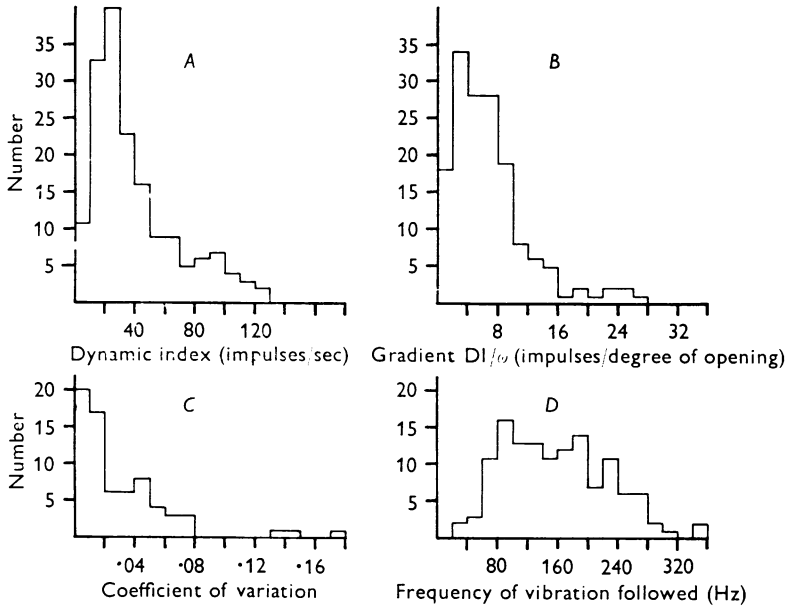

Fig. 3. Distributions of values of (*A*) dynamic index, (*B*) gradient of DI with respect to angular velocity of jaw opening (ω), (*C*) coefficient of variation of impulse intervals at constant muscle length and (*D*) maximal frequency of vibration followed. In all cases fusimotor activity was suppressed by pentobarbitone and chlorpromazine.

derived of DI/velocity by linear regression, and is referred to as 'normalized DI'; (*b*) maximal frequency following during small amplitude sinusoidal stretching at increasing frequencies up to 300 Hz (Brown, Engeberg & Matthews, 1967); (*c*) interspike interval variability (coefficient of variation, CV) during constant maintained stretch (Stein & Matthews, 1965). Responses were always recorded under deep pentobarbitone anaesthesia supplemented by chlorpromazine to suppress fusimotor activity.

The distributions of values of these parameters are plotted in Fig. 3. None of the tests showed a clear separation of units into two groups corresponding to primary and secondary units. Statistical testing showed that the distribution of DI, normalized DI, frequency following and CV were not acceptable as Gaussian but were indistinguishable from lognormal. The histograms of both DI and CV do, however, give some indication of small second peaks. Though these are probably not significant in themselves, the second peak in CV happens to correspond with that found for primary endings by Stein & Matthews (1965).

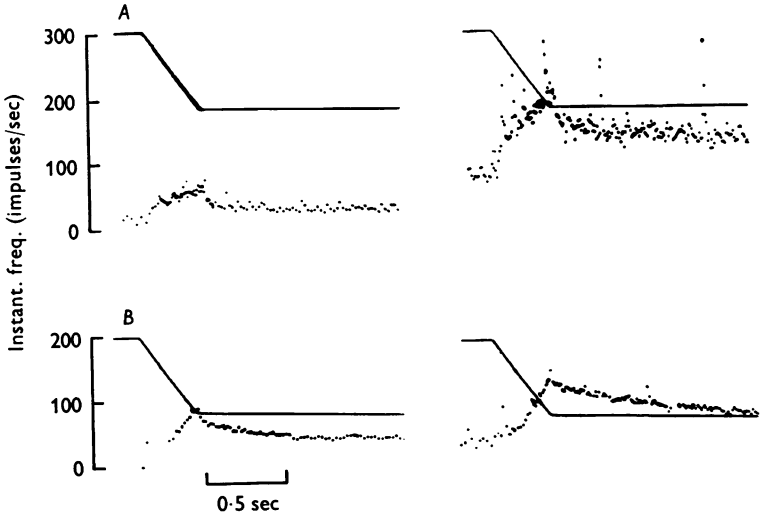

Fig. 4. Responses of the two units, (*A*) pterygoid and (*B*) temporalis, illustrated in Fig. 1 to ramps of jaw opening of 1·5 degrees amplitude. In each case the response on the left is before, and on the right 1 min after, the I.V. administration of 200 μg/kg SCh.

The use of suxamethonium in the classification of spindle units

It was thought that the lack of separation of units into two populations may have been due to many primary units not showing their expected dynamic response in the absence of fusimotor drive. Consequently, in another series of experiments the effect of SCh was tried because it is believed to cause intrafusal contraction especially of nuclear bag fibres, is known to excite primary endings more than secondaries (Fehr, 1965) and has been used previously (Rack & Westbury, 1966) to help classify spindle afferents.

The instantaneous frequency of units was recorded in response to ramps at 1·0, 4·5 and 10·0°/sec, before and after 200 μg/kg SCh I.V. The ramps were timed to begin at respectively 45, 60 and 75 sec after injection.

Artificial ventilation was maintained throughout. SCh administration was followed by an initial reduction or abolition of unitary activity for 5–10 sec. Over the next 30 sec discharge increased irregularly, often being unrelated to muscle extension. Thereafter, the pattern of firing stabilized and correlated with jaw movements. Activation was most consistent at 1 min and subsequently declined to normal at 5–10 min. Comparison of responses before and after SCh was made on the intermediate speed ramp at 1 min.

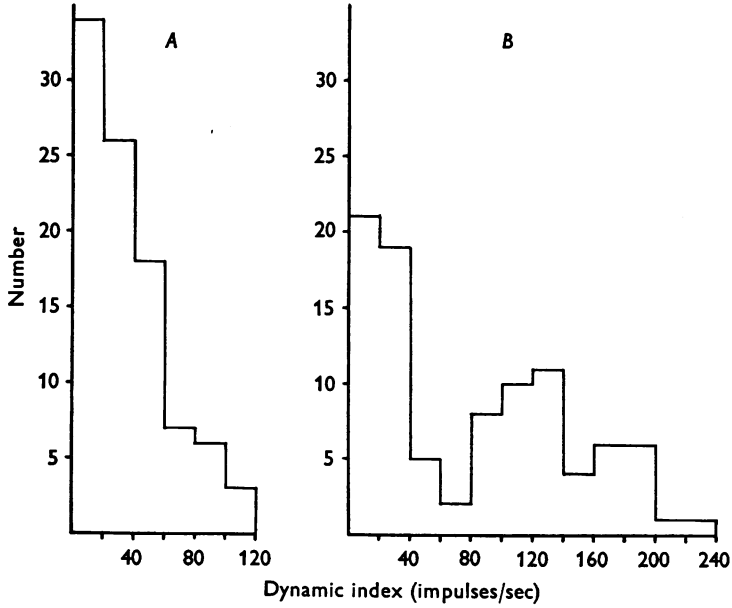

Fig. 5. Distribution of values of DI in ninety-four spindle afferent units (*A*) before, and (*B*) 1 min after 200 μg/kg SCh.

Fig. 4 illustrates the effect of SCh on two units. Initially the DI of both units was similar. After SCh the resting discharge frequency increased. One unit (*A*) showed a large increase in DI and the irregularity of its firing. In contrast there was only a small change in the dynamic response of the other unit (*B*) and its discharge remained regular. These responses resemble those described by Rack & Westbury (1966) for primary and secondary afferents respectively. Histograms of DI for ninety-four units tested in this way at 4·5°/sec are shown in Fig. 5. SCh is seen to convert the single skew (lognormal) distribution into a clearly bimodal one. The two groups thus demonstrated contain approximately equal numbers when pooled from the three muscles. Measurements at the other velocities gave essentially the same results. It seems likely that, as in the work of Rack &

Westbury (1966), the two groups correspond to primary and secondary afferents. Separation of units was clear in both pterygoid and temporalis muscles, but less complete in the masseter. The relative numbers of 'primary' and 'secondary' units were: masseter, 14:20; temporalis, 5:13 and pterygoid, 21:8 respectively.

DISCUSSION

Of the various cell types, thought at times to be present in the MeNV, we have been able to confirm the existence of only two. These are first order somata of tooth mechanoreceptors and of muscle spindles of the jaw-closing muscles. Though failure to find other cell types can never be regarded as totally satisfactory evidence for their absence, the extent of our search makes the presence of eye muscle proprioceptors, jaw-opening muscle proprioceptors or tendon organ afferents extremely unlikely.

It seems that in previous reports of eye muscle receptors (Cooper & Fillenz, 1955; Fillenz, 1955) confusion arose because of the disturbance of masticatory muscle spindles by movements in the orbit, which, in the cat, has no bony posterolateral wall. A wide variety of anatomical evidence summarized by Hosokawa (1961) suggests that eye muscle proprioceptors find their way into the ophthalmic branches of the fifth nerve. This is particularly well seen in the goat in which Whitteridge (1955) and Cooper & Daniel (1957) were able to find separate, purely sensory, nerve bundles passing from eye muscle nerves to fifth nerve branches in the orbit. This being so, there would be general grounds for expecting the afferent cell bodies to be in the trigeminal ganglion. There is direct evidence to this effect in the pig and sheep (Manni *et al.* 1966, 1968). In contrast, the sensory fibres which are well established to by-pass the ganglion and to have their cells in the MeNV, namely the jaw muscle proprioceptors (Corbin & Harrison, 1940; Szentagothai, 1948; Jerge, 1963) enter via the motor root of the fifth nerve (McIntyre, 1951). In the goat, in which evidence is probably best for the existence of eye muscle proprioceptor neurones within the brain stem (Cooper, Daniel & Whitteridge, 1953), responses were located close to the point of entry of the fifth nerve into the pons rather than in the MeNV. Moreover, the latency of 20–50 msec observed for the responses to eye muscle stretch cannot be accepted as good evidence of the cells concerned being first order. The present observations cause us to dismiss the representation of eye muscle proprioception in the MeNV of the cat and to have serious doubts about it in other species.

In most previous work on the MeNV, no special effort has been made to distinguish tendon organs from muscle spindles. Smith (1969) claimed to have shown increased discharge of stretch sensitive units during the rise

of tension in muscle twitches, but his stimuli were restricted to masseter and he did not appreciate that its contraction could excite spindles in the pterygoid muscle. The anatomical studies of Szentagothai (1948) argue against tendon organ representation in the MeNV since mid-brain lesions caused degeneration of spindle but not of tendon organ afferents. If, as would seem to be the case, the first order afferent cell bodies of tendon organs of jaw-closing muscles are not in the MeNV they would be expected to be in the trigeminal ganglion. The failure by Beaudreau & Jerge (1968) to find them there may have been due to the insensitivity of tendon organs to passive stretch of a relaxed muscle (Jansen & Rudjord, 1964). It would be desirable to look for tendon organ afferents again while trying to excite them with muscle twitches.

In the present work, initial attempts to characterize the jaw muscle spindle afferents as belonging to primary or secondary endings on the basis of their dynamic sensitivity were unsuccessful in the absence of fusimotor activation. Neither were vibration following nor variability of discharge of any real help in this situation. Conduction velocity measurements were not feasible, and in any case there is no certainty that the separation of fibres belonging to primary and secondary endings on this basis is possible except in cat hind-limb muscles. However, the histological work of Karlsen (1965) has shown the presence of typical spindles in rat jaw muscles with primary and secondary endings, and in the present work excitation of the spindles by SCh did lead to their clear division into two approximately equal groups on the basis of dynamic index. In the light of this finding, it seems unwise to attempt to separate primaries and secondaries functionally in other situations in the absence of fusimotor drive or of SCh activation. The inability of Koeze (1968) to find two populations of spindle afferents in the baboon tibialis anticus muscle is understandable in these terms.

As a result of this work, it is now fairly certain that all cells recorded in the MeNV can only belong to jaw-closing muscle spindles or tooth receptors. The latter are easily distinguished, so that we have a preparation in which spindle afferents are readily accessible to recording by extracellular electrodes without dissection and with a minimum of interference with the animal.

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