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THE RECRUITMENT ORDER OF γ-MOTONEURONES IN THE DECEREBRATE RABBIT

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SUMMARY

1. The order of firing (i.e. recruitment order) of gastrocnemius medialis γ-motoneurones to natural stimulation of the limbs has been studied in the precollicular decerebrate rabbit.

2. Recruitment order was not invariable. However, when a fixed order occurred there was a significant tendency for neurones to be recruited in order of increasing axonal conduction velocity. The functional significance of this finding is discussed.

3. In the preparation used, many γ-motoneurones were spontaneously active.

4. Two types of γ-motoneurone were distinguished on the basis of their resting discharge characteristics and responses to natural stimulation.

5. A significant correlation between resting discharge frequency and axonal conduction velocity was found for γ-motoneurones that were predominantly excited by natural stimulation.

INTRODUCTION

In contrast to α-motoneurones little is known about the patterns of recruitment displayed by γ-motoneurones. The present study examines the order in which γ-motoneurones begin firing in response to natural stimulation. Axonal conduction velocity has been used as an index of motoneurone size since this relation is well established for α-motoneurones (Barrett & Crill, 1971; Cullheim, 1978) and recent studies suggest that it also holds for γ-motoneurones (D. R. Westbury, personal communication; Cullheim & Ulfhake, 1979).

In the preparation used (ie. decerebrate rabbit), some γ-motoneurones were spontaneously active in the absence of intentional stimuli. In addition to studying the recruitment order of silent units, tonically firing neurones were also recorded and the relation between axonal conduction velocity and resting discharge frequency examined.

There are two types of functionally distinct γ-motoneurones (Matthews, 1962), static and dynamic, which differ in synaptic input (Jansen & Matthews, 1962*a*; Appelberg & Emonet-Dénand, 1965). Since both types are active in the decerebrate preparation (Jansen & Matthews, 1962*b*), the possibility that they may display different patterns of response to natural stimulation was examined. γ-motoneurones did exhibit two patterns of response to natural stimulation and the results are presented in the light of this finding.

A preliminary account of some of this work has been published (Murphy, 1978).

METHODS

The preparation

Experiments were performed on eighteen adult rabbits (1·7–2·9 kg) of the New Zealand Red or White variety. Anaesthesia was induced by I.V. methohexitone (Brietal, Lilly & Co.), and continued by inhalation of fluothane (Halothane, I.C.I.). After decerebration, anaesthesia was discontinued and the animal was paralysed with gallamine triethiodide (Flaxedil, May & Baker). Respiration was maintained using a pump and the preparation allowed to recover from the anaesthetic for at least one hour before recordings were made.

The sciatic nerve was exposed and a paraffin oil pool constructed from skin flaps. The pool temperature was maintained in the range 34–38 °C. Rectal temperature was maintained in the range 36–38 °C.

Isolation and identification of γ-motoneurones

Electrical recordings were made from the cut gastrocnemius medialis nerve and all other nerves were left intact. Functionally single, reflexly responsive γ-motoneurones were isolated in dissected filaments of the nerve and identified by the conduction velocities of their axons, which ranged from 9–44 m/sec. Additionally, in the decerebrate preparation, γ-motoneurones may be characterized by their low threshold to skin stimulation (Hunt, 1951). Generally, two functionally single units were recorded at the same time. However, occasionally, where the signal-to-noise ratio allowed good separation, a third unit was recorded on one of the electrodes.

The axonal conduction velocity of each unit was calculated from the latency of response to electrical stimulation of the muscle nerve and the conduction distance (range, 25–36 mm). The error in individual latency measurements was estimated to be ±0·05 msec. No allowance was made for initiation time of the action potential, which is known to range from 0 to 0·1 msec in the preparation used (Ellaway, Murphy, Pascoe & Read, 1978). Thus the maximum error in measuring the conduction latency of a unit was +0·05 and −0·15 msec. When the latencies of two units were compared, it was not therefore possible to determine their relative conduction velocities if the difference was less than 0·2 msec (i.e. 0·05 + 0·15 msec), since the apparent difference may then have been wholly due to experimental error. Conduction velocities were corrected to 37·5 °C using a temperature coefficient of 1·32 which is the Q_{10} value for nerve (Franz & Iggo, 1968).

Recording and analysis of nerve impulses

Nerve activity was amplified by conventional means and displayed on an oscilloscope, the output of which was stored on magnetic tape for subsequent photography (e.g. Fig. 4). The frequency of action potentials could be monitored by converting them into standard pulses which were fed to an integrator (time constant of decay, 180 msec) whose d.c. voltage output was directly proportional to the frequency of the incoming train of pulses. However, when two or more units were recorded at the same time, their frequencies were measured from photographic records.

The pattern of discharge of some γ-motoneurones was examined by constructing sequential interspike interval histograms using a computer (LINC-8, Digital). This form of presentation allowed an appreciation of the mean frequency of discharge of a neurone and the relative constancy of this parameter.

Application of stimuli

Natural stimulation was used as a means of producing reflex responses in γ-motoneurones. The following stimuli were routinely employed:

(i) touching and stroking the fur over the following skin areas: (*a*) the dorsolateral surface of both ipsi- and contralateral forelimbs, (*b*) the area innervated by the sural nerve of the ipsi- and contralateral hind limbs (i.e. the lateral posterior leg, from the knee to the ankle, and the lateral side and plantar surface of the foot), and (c) the skin over the back and dorsal surface of the neck;

(ii) pressure, ranging from light to heavy and noxious pinching, applied manually to the following areas: (*a*) ipsi- and contralateral forepaws, and (*b*) ipsi- and contralateral hind limbs, particularly the toes, heel and Achilles tendon.

The area of stimulation was not carefully mapped and no strict attempt was made at either quantifying the stimuli employed, or restricting their influence to a specific receptor modality.

RESULTS

A reciprocal effect on γ-motoneurone discharges

Natural stimulation produced two patterns of response in the discharges of the γ-motoneurones. Some stimuli produced only predominant excitation, while others produced a reciprocal effect (Fig. 1) in which some neurones showed predominant excitation at the same time as others were strongly inhibited.

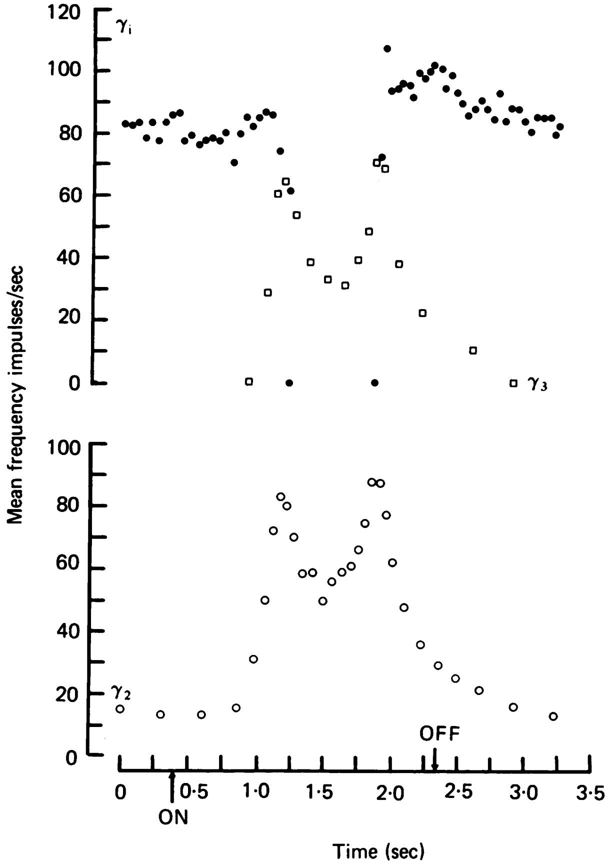

Fig. 1. A reciprocal effect in the discharges of three G.M. γ-motoneurones (axon conduction velocities: γ_1 (●), 19 m/sec; γ_2 (○), 23 m/sec; γ_3 (□), 35 m/sec) produced by pinching of the left forepaw. The neurones were recorded at the same time. Mean frequency was calculated over four consecutive interspike intervals. The arrows represent the onset (ON) and removal (OFF) of the stimulus.

Pinching the forepaws was a particularly effective way of eliciting the reciprocal response. Forty-three units showed a pattern of response similar to that of γ_1 of Fig. 1 in which their discharge could be completely inhibited for a brief period (range, 0·6–2·0 sec). Sixty-three other neurones displayed excitatory responses similar to those of either γ_2 or γ_3, also shown in Fig. 1. These opposite responses occurred in the same animals at the same time. The presence of such a reciprocal effect on these neurones suggests that their synaptic inputs differ, and is consistent with the hypothesis that they might constitute two functionally distinct types of γ-motoneurone. Henceforth, for convenience, neurones which displayed a pattern of response similar to that of γ_1 in Fig. 1 will be referred to as γ-inhibited, while those which behaved in a similar fashion to γ_2 or γ_3 in this Figure will be called γ-excited.

No tonically firing α-motoneurones were encountered. Presumed α activity (as identified by relatively large spike size), however, could be evoked in some nerve filaments. In the forelimb (always) and hind limb (generally) the intensity of natural stimulation required to elicit such discharges was greater than that necessary to produce the reciprocal response.

Resting discharge characteristics of γ-motoneurones

Although the conduction velocities of the two types overlapped (γ-inhibited, 9–44 m/sec; γ-excited, 13–43 m/sec), their resting discharge characteristics differed.

Both types of γ-motoneurone could be made to discharge at frequencies in excess of 100 impulses/sec by natural stimulation of the limb. γ-inhibited units had mean resting frequencies in the range 0–90 impulses/sec, whereas spontaneously firing γ-excited units with mean frequencies greater than 42 impulses/sec were never encountered. γ-excited neurones not only discharged over a smaller, lower range but, generally, their spontaneous firing rates were lower. Thus from a total of eighty-one pairs of units, in which both types were recorded at the same time, in seventy-seven instances the γ-inhibited unit had the higher mean frequency. The results of a typical experiment are shown in Fig. 2.

Fig. 2. Mean resting frequencies of γ-excited (○) and γ-inhibited motoneurones (●). Each line represents a pair of units recorded at the same time. Note that in every case the γ-inhibited motoneurone discharged at the higher mean rate. The results are from an experiment in which ten pairs of units were recorded involving nine different neurones (five γ-excited and four γ-inhibited).

The patterns of discharge of tonically firing γ-motoneurones were examined by constructing sequential interspike interval histograms. γ-inhibited and γ-excited neurones tended to exhibit one of two discharge patterns found. In most γ-inhibited neurones (thirty-three of thirty-four) the mean frequency was relatively fixed and the variability in discharge appeared as an interval by interval fluctuation (Fig. 3*A*).

In contrast, most γ-excited neurones (twelve of fourteen) did not appear to have a fixed mean interval and the variability of the discharge was composed of both an interval-by-interval fluctuation, and trends towards longer and shorter intervals (Fig. 3*B*). The periods of such swings in frequency were generally irregular and did not correspond either to the stroke frequency of the respiration pump or heart rate. These differences in the discharge characteristics of γ-excited and γ-inhibited neurones support the conclusion that they differ in synaptic input.

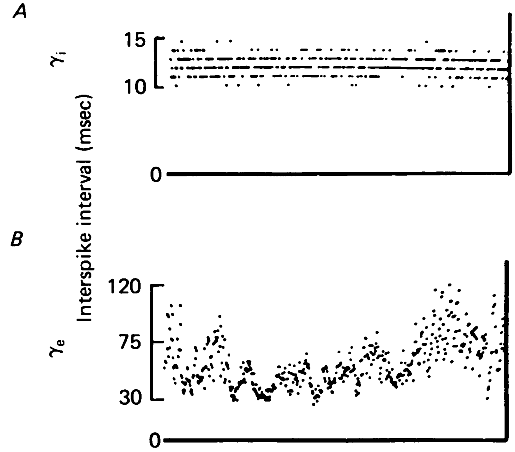

Fig. 3. Sequential interspike interval histograms illustrating the two patterns of tonic γ-motoneurone discharge encountered: *A*, fixed mean frequency (γ-inhibited unit (γ_i), 21 m/sec); *B*, varying mean frequency (γ-excited unit (γ_e) 25 m/sec). Both histograms were constructed from 512 consecutive intervals.

Relation between resting discharge frequency and axonal conduction velocity

Tonically firing γ-motoneurones showed no fixed relation between axonal conduction velocity and mean resting frequency. In 55·3 % of the pairs (twenty-one out of thirty-eight), the unit with the lower velocity discharged at a higher rate, while in the remainder the converse was true. Since the possible presence of more than one type of γ-motoneurone may have been a complicating factor, the pairs were considered separately, according to the nature of the units involved (i.e. γ-excited/γ-excited, γ-inhibited/γ-inhibited or γ-excited/γ-inhibited). Even within these sub-groups no obvious relation was evident.

A significant ($P <$ 0·003) relation between conduction velocity and resting frequency was found, however, when silent and tonically firing γ-excited neurones were examined. In all twelve of these pairs the tonically firing unit had the lower conduction velocity. Only one silent and one tonically firing γ-inhibited neurone could be compared since these units tended to exhibit a background discharge. Consequently, for the forty γ-excited/γ-inhibited pairs examined it was always the γ-excited unit that was silent.

Recruitment order of γ-motoneurones

A unit was considered to be recruited first if it fired one or more impulses before another, and the recruitment order was assessed, on average, over thirty trials (range, twenty-five to forty). Two patterns of recruitment were observed among forty-one neurones which were all classified as γ-excited on the basis of their responses to natural stimulation. In 51·2% of the pairs (twenty-one out of forty-one) the recruitment order was fixed; the same unit was consistently recruited first (and dropped out last) in repeated trials (Fig. 4*A* and *B*). For the remaining twenty pairs either unit could begin firing first, so that the recruitment order was variable. Generally, either unit could also drop out last, although in two pairs the same unit dropped out last every time. The rate of stimulus application was not strictly controlled, but there seemed to be no obvious tendency for the order of recruitment to be dependent on this variable. Thus γ-motoneurones do not always show a fixed recruitment order to natural stimulation.

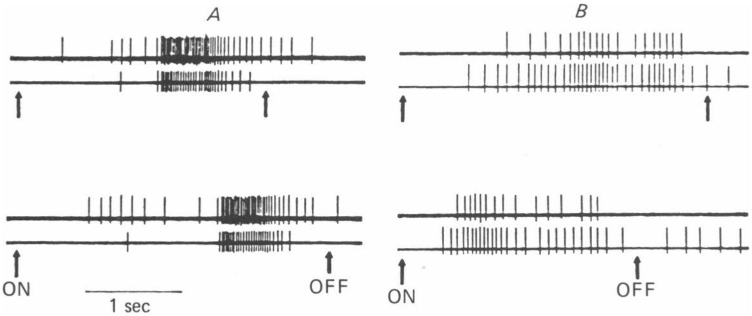

Fig. 4. Two examples of fixed recruitment order of γ-motoneurones to natural stimulation applied between the arrows. In *A*, the unit with the lower conduction velocity (upper trace, 34 *vs.* 38 m/sec) is recruited first to pinching of the left forepaw. In *B*, the unit with the higher velocity (lower trace, 35 *vs.* 28 m/sec) fires first to stroking of the left forepaw. Twelve pairs of neurones had the recruitment pattern illustrated in *A*, whereas only one pair had the pattern shown in *B*.

In 54·2% (thirteen) of the pairs in which the relative conduction velocities of the units were known (i.e. latency difference greater than 0·2 msec) the order of recruitment was fixed and in the remainder it was variable. A variable pattern was not restricted, therefore, to units having similar conduction velocities, as might be predicted from the size principle (Henneman, Clamann, Gillies & Skinner, 1974). Of the thirteen pairs showing a fixed order of recruitment, in twelve instances the unit with the lower conduction velocity was consistently recruited first (Fig. 4*A*). The probability of this result occurring by chance is less than 0·003 indicating that when γ-motoneurones do show a fixed recruitment order, there is a significant tendency for it to occur in order of increasing conduction velocity.

DISCUSSION

Recruitment order of γ-motoneurones

This study has shown that the order of firing of γ-motoneurones to natural stimulation is not always fixed. However, when a fixed recruitment pattern is the case, there is a significant tendency for it to occur in order of increasing axonal conduction velocity, and presumably cell size. Under these conditions, therefore, the recruitment order of γ-motoneurones conforms to the size principle.

Exceptions to the size principle have been found in studies of α-motoneurone recruitment in the cat when natural stimulation was used (Wyman, Waldron & Wachtel, 1974; Kernell & Sjoholm, 1975). However, α-motoneurones frequently show a size-dependent recruitment order to various electrical, physiological and natural stimuli (Burke & Edgerton, 1975). This seems to be particularly true during slowly increasing, isometric voluntary contraction in man (Milner-Brown, Stein & Yemm, 1973; Stephens & Usherwood, 1977). During such voluntary contractions, muscle spindle endings are recruited at fixed tension levels (Burke, Hagbarth & Skuse, 1978), indicating that 'the threshold for activation of a spindle ending in an isometric voluntary contraction is determined by its fusimotor innervation, and that fusimotor neurones probably have a recruitment order, much as do skeletomotor neurones'.

While the present results show directly that γ-motoneurones may exhibit a fixed recruitment order similar to that of α-motoneurones, it is also clear that under some conditions the recruitment order of γ-motoneurones is variable. Little can be said about the factors producing this variability except that similarity of cell size and rate of stimulus application do not appear to be associated with it. For α-motoneurones both these factors have been reported to affect recruitment order (Grimby & Hannerz, 1968; Henneman *et al* 1974). It should be noted that the recruitment order of only one type of γ-motoneurone was studied (i.e. γ-excited) since the other type (i.e. γ-inhibited) was generally spontaneously active. Further, it is not known if this classification corresponds with the accepted functional division into static and dynamic fusimotor fibres (Matthews, 1962).

Among the units showing a fixed order of recruitment there was a significant tendency for firing to occur in order of increasing motoneurone size, as indicated by axonal conduction velocity. This relation probably depends on a number of factors concerning both the organization of synaptic input and the intrinsic properties of the cells involved (Burke & Edgerton, 1975). For α-motoneurones such a recruitment pattern has the functional advantage of permitting relatively fine control of muscle tension during graded contraction (Henneman & Olson, 1965), while allowing a muscle to participate in a range of activities demanding different types of contraction (Henneman, Somjen & Carpenter, 1965; Stephens & Stuart, 1975; Stephens & Usherwood, 1977). These advantages are a consequence of the fact that, generally speaking, slowly contracting motor units tend to have lower axon conduction velocities, develop less tension and exhibit greater resistance to fatigue than fast contracting units (Henneman *et al.* 1965; Burke, 1975; Stephens & Stuart, 1975).

In contrast to α-motoneurones, the functional advantage(s) of a size dependent recruitment order of fusimotor neurones is not obvious, since there is no known correlation between the size of a γ-motoneurone and its functional, or anatomical, properties. The two types of functionally distinct fusimotor fibre, static and dynamic, have overlapping conduction velocities (Brown, Crowe & Matthews, 1965; Ellaway, Emonet-Dénand, Jami & Joffroy, 1972). Further, there have been no reports of any relation between the size of a γ-motoneurone and either the number of spindles or afferents it affects, or the strength of its action on a particular ending. It should be emphasized, however, that such correlations have not been sought systematically. In addition, since a given γ-motoneurone may influence more than one spindle ending, some assessment of the over-all effect on spindle discharge of stimulating individual fusimotor fibres would be of particular relevance to this discussion.

At present the available evidence argues against there being any significant relation between the size of a γ-motoneurone and its functional properties. If this is the case then a size-dependent recruitment order of fusimotor neurones might simply represent a convenient method of gradation in this system.

Relation between resting discharge frequency and axonal conduction velocity

The spontaneous activity of γ-motoneurones is a well known feature of many laboratory preparations including anaesthetized, decerebrated and spinalized cats and rabbits (Hunt, 1951; Hunt & Paintal, 1958; Voorhoeve & Van Kanten, 1962; Diete-Spiff, Dodsworth & Pascoe, 1962). However, the factors responsible for this feature of some of the γ-motoneurone population are not clear. In accordance with the size principle one might expect spontaneously active neurones to be smaller than silent units. While such a tendency has been shown to exist in the present study, it is obscured by the presence of neurones which differ in their synaptic inputs. Both these factors (i.e. cell size and synaptic input) are probably important in determining which γ-motoneurones exhibit spontaneous activity.

Tonically firing γ-motoneurones, regardless of their type, showed no relation between size and firing frequency. This lack of correlation could be explained if non-synaptic factors (e.g. after-hyperpolarization duration) are able to influence the excitability of tonically firing γ-motoneurones, leading to a complex relation between cell size and discharge rate. This seems to be true of α-motoneurones where the duration of after-hyperpolarization is related to both the gain (Kernell, 1966), as measured by the amount of injected current required per unit increase in firing rate, and size (Eccles, Eccles & Lundberg, 1958) of the neurone. γ-motoneurones also possess an after-hyperpolarization (Eccles, Eccles, Iggo & Lundberg, 1960; Gustafsson & Lipski, 1979; Kemm & Westbury, 1978). However, due to the difficulties involved in impaling these cells with a micro-electrode, there is little information concerning the interrelations of after-hyperpolarization duration and cell size or gain.

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