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DISTRIBUTION OF MONOSYNAPTIC Ia EXCITATORY POST-SYNAPTIC POTENTIALS IN THE MOTOR NUCLEUS OF THE CAT SEMITENDINOSUS MUSCLE

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SUMMARY

1. Evidence is presented for a lack of localization of monosynaptic Ia excitatory post-synaptic potentials (e.p.s.p.s) in the motor nucleus supplying the atypical cat hind limb muscle semitendinosus, which has anatomically distinct in-series compartments.

2. Recordings were made from dorsal root filaments containing functionally isolated Ia, spindle group II and Ib axons from the proximal and distal compartments of semitendinosus. Twitch of either of these in-series compartments resulted in accelerated discharge of Ia and spindle group II fibres in the other compartment. Ib fibres of either compartment showed an in-series response to twitch of a single compartment which was weaker than twitch of the whole muscle, a finding which was consistent with the diminished force produced by twitch of either compartment alone.

3. In addition, intracellular recordings were made from semitendinosus motoneurones in anaesthetized low-spinal cats during electrical stimulation of the nerve branches to proximal semitendinosus and distal semitendinosus. Comparison of proximal semitendinosus and distal semitendinosus motoneurones failed to reveal any difference between the two cell groups with respect to the average Ia e.p.s.p. amplitude produced by either the proximal or distal semitendinosus nerve branch. However, e.p.s.p.s due to stimulation of distal semitendinosus were approximately 65% larger, on average, than those due to stimulation of proximal semitendinosus in either motoneurone group.

4. Analysis of cell location along the rostro-caudal axis of the spinal cord indicated that the proximal and distal semitendinosus cell groups are largely co-extensive.

5. Recordings of volleys in the proximal and distal semitendinosus nerve branches in response to stimulation of the L6, L7 and S1 dorsal roots showed that group I afferents from the proximal semitendinosus compartment tend to have a more rostral entry point to the spinal cord than do distal semitendinosus afferents.

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6. E.p.s.p. amplitude in either cell group due to stimulation of either nerve branch showed little dependence on cell location in the spinal cord.

7. The results are discussed with respect to the relation between muscle function and the distribution of monosynaptic Ia connexions.

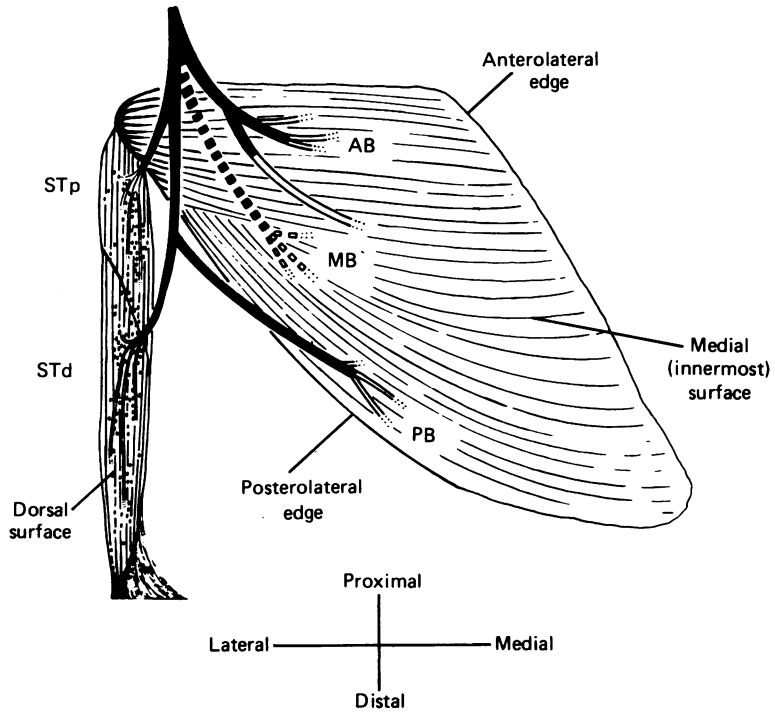

Fig. 1. A dorsal view of the gross architecture and nerve branch patterns of the biceps femoris and semitendinosus muscles. The semitendinosus drawing is redrawn from one in Chin *et al.* (1962; part of their Fig. 2). It shows a dorsal view of the left semitendinosus muscle of a kitten and the diagonal intramuscular tendon which separates semitendinosus into a proximal (STp) and distal (STd) compartment. Skeletomotor muscle fibre orientation is sketched, together with the distribution of spindle capsules (black oval symbols). The nerve supply is shown in black up to the point of entry of nerve branches into the muscle. Biceps femoris is drawn with its medial (innermost) surface exposed by reflexion of the muscle's anterolateral border to show the nerve branches to the anterior (AB), middle (MB) and posterior (PB) portions of the muscle. The dashed line to the middle part of biceps femoris represents an alternate innervation found in some animals (Botterman *et al.* 1983).

INTRODUCTION

In the previous paper (Botterman, Hamm, Reinking, & Stuart, 1983), a localized Ia projection was demonstrated in the spinal motor nucleus supplying the cat biceps femoris muscle. A similar result was obtained by Brink, Jinnai & Wilson (1981) for motor nuclei of biventer cervicus and splenius, dorsal neck muscles which are innervated by separate nerve branches from several spinal segments (Richmond & Abrahams, 1975). In the motor nucleus of medial gastrocnemius, a localization of Ia e.p.s.p.s was reported by Lucas & Binder (1981) in a study of composite e.p.s.p.

amplitudes, and by Lucas, Cope & Binder (1982) in a study of single-fibre e.p.s.p.s employing spike-triggered averaging. However, Munson, Fleshman, Sypert & Zengel (1981) found little evidence for such localization in a study also using spike-triggered averaging. In another study employing spike-triggered averaging, no difference was reported between the effects of single Ia afferents on the groups of motoneurones supplying the two compartments of the semitendinosus muscle (Nelson & Mendell, 1978). Thus, the existence of localized Ia projections, suggested originally by Cohen's findings (1953, 1954) of reflex localization in rectus femoris and vastus intermedius, has been established in the motor nuclei of several muscles, although not in every case examined.

The mixed results from these studies raise the issue of whether the localization of Ia projections is a general principle in the organization of monosynaptic Ia connexions or is a specialization of particular motor nuclei. In this regard, the structure of semitendinosus deserves comment. It is composed of anatomically distinct in-series compartments, divided by a tendinous inscription and innervated by separate branches of the semitendinosus muscle nerve (Chin, Cope & Pang, 1962; English & Letbetter, 1981). The structure of semitendinosus, which is atypical for the hind limb, is illustrated in Fig. 1 and contrasted there with that of biceps femoris, which has a more common arrangement of muscle fibres lying largely in parallel. Given this marked difference in structure between these two muscles, a corresponding difference in the organization of their motor nuclei might serve as the basis for the presence of localization in one case and its absence in the other. This possibility was the motivation for the present study, in which the functional aspects of semitendinosus's anatomy have been examined by recording the responses of muscle receptors to twitches of the separate and combined muscle compartments, and in which the distribution of Ia monosynaptic e.p.s.p.s in the semitendinosus motor nucleus has been examined by recording composite e.p.s.p.s due to stimulation of the nerve branches to the proximal and distal semitendinosus muscle compartments. These studies demonstrate a functional correlate of semitendinosus's in-series arrangement in the response of muscle receptors to twitch and a lack of localization of Ia projections, although there is also evidence of a limited topographic organization of the motor nucleus.

Preliminary communications of this study have been presented (Botterman, Hamm, Reinking & Stuart, 1980, 1981).

METHODS

Experiments were performed on adult cats (2–3·2 kg in weight). Anaesthesia was induced using a mixture of 1–2% halothane, nitrous oxide and oxygen. This anaesthesia was continued for the course of the two experiments on receptor responses, or was replaced with chloralose–urethane in the twenty-three intracellular experiments, as described in the preceding paper (Botterman *et al.* 1983). Sixteen of the animals used in this series of intracellular experiments also contributed data to the preceding paper (Botterman *et al.* 1983).

Experiments on responses of muscle receptors. The surgical techniques, animal fixation, temperature regulation, measurement of muscle twitch forces, and the identification of muscle afferents have been described in previous reports (Stuart, Goslow, Mosher & Reinking, 1970; Stuart, Mosher, Gerlach & Reinking, 1970, 1972; Stephens, Reinking & Stuart, 1975). Muscle afferents were functionally isolated in dorsal root filaments after section of the L6, L7 and S1 dorsal roots. Spindle

afferents were classified as Ia, Sp II or unclassified for conduction velocities of greater than 75 m/s, less than 60 m/s, or between 60 and 75 m/s, respectively.

The muscle nerve branches to proximal semitendinosus and distal semitendinosus were carefully dissected free of connective tissue and suspended on spring-mounted monopolar electrodes for stimulation. These electrodes were referred to an indifferent electrode in adjacent, denervated thigh musculature. Stimulus strength was graded just high enough to ensure the maximum twitch in one compartment without spread of stimulus current, as judged by the absence of a twitch in the in-series compartment. Reference length (L_0) was chosen as the muscle length at which a maximum twitch was obtained in response to stimulating both nerve branches. Stimuli were applied at a mean interval of 1·13 s using a Geiger counter-triggered random pulse generator (range of intervals from 1·03 to 1·21 s). Receptor responses to twitch of the whole muscle or of either muscle compartment were obtained at L_0.

Data were recorded on FM magnetic tape for subsequent analyses. Muscle twitches and afferent spikes during the time course of the twitch were accumulated in a signal averager. The spikes were accumulated in 1 ms bins using a pulse count input after the original afferent recording had been passed through a window discriminator. The afferent histograms and averaged twitches were then transferred to a small laboratory computer for construction of histograms with suitable bin widths.

Intracellular experiments. Ia monosynaptic e.p.s.p.s were evoked in semitendinosus motoneurones by stimulation of sectioned semitendinosus nerve branches using bipolar electrodes. The methods used in these experiments have been described in the preceding paper (Botterman *et al.* 1983). Out of the twenty-three intracellular experiments on semitendinosus, thirteen were selected to contribute e.p.s.p. data to the present study. E.p.s.p. data from the other experiments were rejected without further analysis due to an insufficient yield of cells with complete sets of tests and suitable resting potentials.

In the last six experiments (ninety-eight cells), intracellular records were obtained at high gain using a sample-and-hold amplifier (Reinking & Stephens, 1975). Use of this amplifier provided a recording of the intracellular signal without the distortion associated with the low-frequency cut-off of a conventional a.c.-coupled amplifier. In these instances, correction of own-branch e.p.s.p. records for the contribution of the M spike was accomplished using an averaged M spike wave form which had been recorded using the sample-and-hold amplifier (Hamm, Botterman, Reinking & Stuart, 1983). As in the previous study (Botterman *et al.* 1983), other-branch e.p.s.p.s were compared with and without current passage. A significant difference was not found in the experiments utilizing the sample-and-hold amplifier, while e.p.s.p.s recorded during the injection of hyperpolarizing current were less than those without current in the experiments using conventional a.c. recording (mean difference of 0·27 mV; standard error of 0·08 mV). This difference was attributed to overcompensation in the correction (fitted by eye) of the slope in the e.p.s.p. record due to decay of the voltage transient resulting from current injection. The amplitudes of e.p.s.p.s recorded during current passage with a.c.-coupled amplification were adjusted by this amount.

Values of input resistance include seventy-five determined according to the shift in membrane potential during current passage and five determined by the spike-height method (Frank & Fuortes, 1956). Input resistance values were accepted according to the criteria given in the preceding paper (Botterman *et al.* 1983). In two experiments (twenty-one cells), these values were not measured owing to an inadvertent failure to record the amplitude of current being passed.

RESULTS

Afferent responses to twitch of semitendinosus compartments

The in-series arrangement of semitendinosus's muscle compartments is readily evident in the responses of muscle afferents to separate twitches of the individual compartments. Characteristic responses are shown for Ia and Ib afferents in Fig. 2. These results are typical of the entire data base from two experiments, comprising responses of ten Ia, nine Ib and ten spindle group II afferents.

The left of Fig. 2 shows spindle responses to twitch of their own compartments, in-series compartments, and of the whole muscle. The spindle responses to own-

compartment twitch display a typical pause during the rising phase of the twitch. This is in contrast to the accelerated discharge which occurs during twitch of the in-series compartment. The responses during twitch of the whole muscle demonstrate the dominance of the local environment on receptor response as both proximal and distal semitendinosus Ia afferents pause during the twitch. Qualitatively similar responses were found for spindle group II afferents.

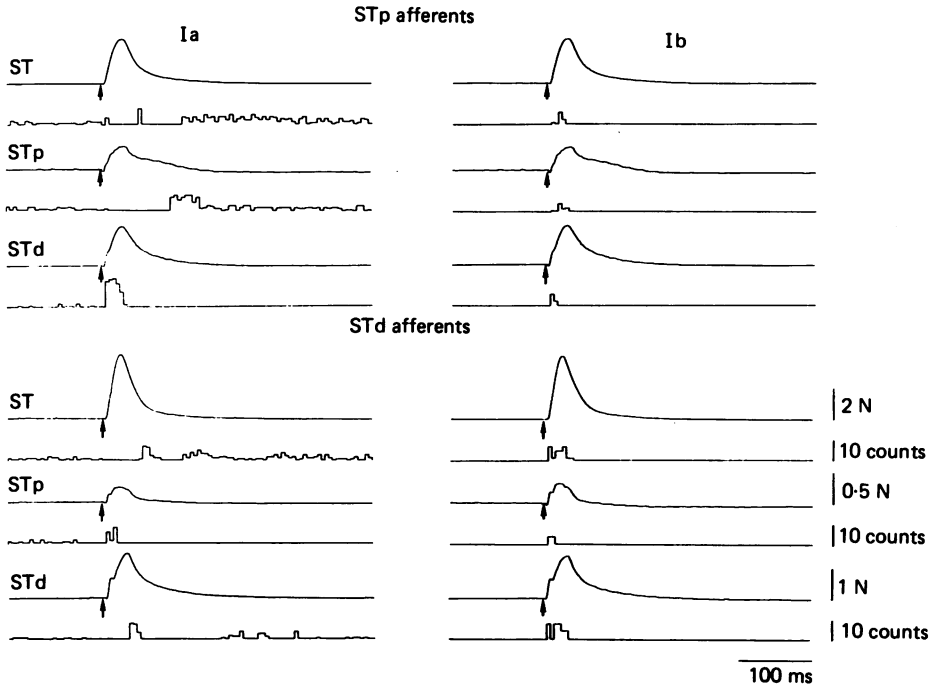

Fig. 2. Typical patterns of muscle receptor response to separate twitch of the two compartments of semitendinosus. Each quadrant contains three pairs of records giving muscle twitch and afferent response to random stimulation of the semitendinosus muscle nerve, the proximal semitendinosus nerve branch, or the distal semitendinosus nerve branch. Upper trace of each pair shows the averaged ($n = 8$) twitch response with muscle length set to give the peak whole muscle twitch. The arrows below each record give the time of stimulus. Lower traces show pre- and post-stimulus time histograms with vertical calibrations showing total number of occurrences/5 ms bin of afferent firing during the course of the same eight consecutive twitches. Responses of Ia afferents located in proximal semitendinosus (top) or in distal semitendinosus (bottom) are shown to the left, while responses of Ib afferents are shown to the right. The 'direct spikes' due to the electrical stimulus have been deleted from these histograms. The in-series arrangement of this muscle is evident both in the weak twitch response due to contraction of a single compartment and in the increased discharge rate of a spindle due to contraction of its in-series compartment.

Ib afferent responses to whole and compartmental muscle twitch are shown on the right of Fig. 2. A typical burst of discharge can be seen during own-compartment and whole-muscle twitch. To a lesser degree, discharge is also present during twitch of the in-series compartment. This response can be compared with that expected of a Ib afferent to contraction of a portion of muscle lying 'in parallel' to the receptor,

in which either no response would occur or possibly an unloading response would be found (Stuart *et al.* 1972; Binder, 1981).

The in-series arrangement of semitendinosus is evident also in the twitch force produced by either compartment alone. The peak force produced under these circumstances is less than that obtained by whole-muscle twitch and is somewhat less

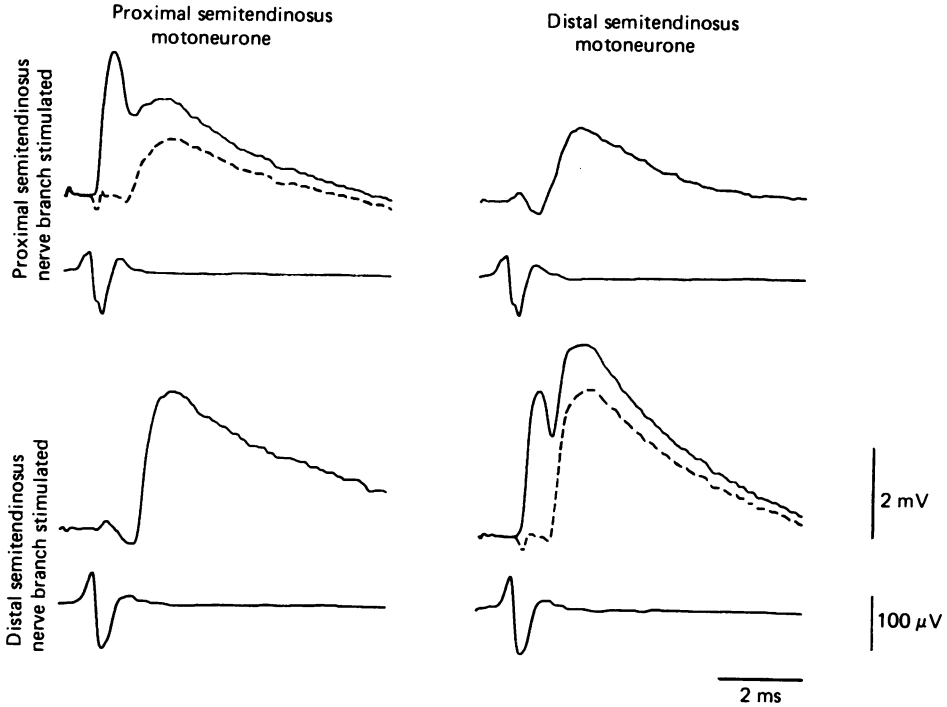

Fig. 3. Composite e.p.s.p.s recorded in proximal semitendinosus and distal semitendinosus motoneurones. The e.p.s.p.s produced by stimulation of the proximal and distal semitendinosus nerve branches in individual proximal semitendinosus (left) and distal semitendinosus motoneurones (right) are displayed. Below each intracellular trace is the dorsal root recording. The own-branch e.p.s.p.s were recorded during the passage of hyperpolarizing current to produce an M spike. The original own-branch records are indicated by continuous lines, while the records which have been corrected for the M spike are shown by dotted lines.

for contraction of proximal semitendinosus than for contraction of distal semitendinosus. This diminished efficacy of the twitch is clearly due to the effect of the additional series compliance (Hill, 1951; Brown & Matthews, 1960) which is present in the form of the inactive muscle compartment.

The test for localization of Ia e.p.s.p.s

Maximum monosynaptic Ia e.p.s.p.s were produced in proximal and distal semitendinosus motoneurones by electrical stimulation of the proximal and distal semitendinosus nerve branches. Typical recordings are displayed in Fig. 3. In both the proximal and distal semitendinosus cells, the e.p.s.p. from the distal branch can

be seen to be larger than that from the proximal branch. Below each e.p.s.p. record is the dorsal root volley recorded for the stimulation of the nerve branch producing that e.p.s.p. These records show a difference in volley size of the proximal and distal semitendinosus branches corresponding to the difference in e.p.s.p. amplitudes due to these branches. Recordings from individual cells provided no evidence for the localization of Ia monosynaptic e.p.s.p.s in semitendinosus in that similar differences in e.p.s.p. amplitude due to the proximal and distal semitendinosus nerve branches were usually observed in motoneurones of both groups.

TABLE 1. Mean composite Ia e.p.s.p.s evoked by stimulation of semitendinosus muscle nerves

	Proximal semitendinosus cells ($n = 53$)	Distal semitendinosus cells ($n = 98$)
Resting potential	56·0 ± 2·1	56·2 ± 1·3
Input resistance	0·86 ± 0·08 (33)	0·79 ± (0·08) (47)
Branch stimulated	E.p.s.p. amplitudes	
Proximal semitendinosus	1·80 ± 0·16	1·69 ± 0·12
Distal semitendinosus	2·85 ± 0·24	2·90 ± 0·21

Resting potential (in mV), input resistance (in MΩ) and e.p.s.p. (in mV) values are expressed as mean ± S.E. of mean (with number of cells in parentheses for input resistance). No correction for the number of afferents in the two nerve branches is required if comparisons are limited to the effects of each nerve branch on the different cell groups

A more conclusive test for the presence of localization requires a comparison in which the difference in e.p.s.p. amplitudes due to unequal contributions of the proximal and distal semitendinosus nerve branches is obviated (cf. Botterman *et al.* 1983). Table 1 presents the average Ia e.p.s.p. values for proximal and distal semitendinosus motoneurones due to nerve branch stimulation. By separately comparing the e.p.s.p. amplitudes produced in proximal and distal semitendinosus cells by each nerve branch, the unequal effect of the nerve branches can be bypassed. Such comparisons show that the proximal semitendinosus nerve branch produces monosynaptic Ia e.p.s.p.s of equal magnitude in proximal and distal semitendinosus motoneurones and that equal e.p.s.p. amplitudes are also produced in both cell groups by the distal branch, indicating that localization of Ia projections is absent between motoneurones supplying the in-series compartments of semitendinosus. Our study of composite e.p.s.p.s thereby confirms the findings of Nelson & Mendell (1978) based on single fibre Ia e.p.s.p.s.

Table 1 confirms the difference in potency of the proximal and distal semitendinosus nerve branches which was suggested by Fig. 3. This finding was unexpected in view of reports of an equal number of spindle capsules in the two compartments of semitendinosus (Chin *et al.* 1962) and of individual Ia afferents from the two compartments projecting equally to motoneurones of those two compartments (Nelson & Mendell, 1978). However, in the thirteen experiments contributing e.p.s.p. data to this study, the dorsal root volley from the distal branch was on average 1·4 times greater in amplitude than that from the proximal branch of semitendinosus,

suggesting that the number of I a afferents is greater from distal semitendinosus than from proximal semitendinosus.

The normalization employed in the preceding paper (Botterman *et al.* 1983) was also applied to the data in this paper. Each e.p.s.p. was divided by the sum of the proximal and distal semitendinosus e.p.s.p.s for each cell to obtain a fractional e.p.s.p. While mean e.p.s.p. amplitudes were not larger on average for one cell group compared to another, the variance associated with each set of e.p.s.p.s was generally larger, and the normalization was used to reduce the effect of this variance in the comparison of mean amplitudes (cf. Lucas & Binder, 1981). Analysis of the differences between cell groups of the mean fractional e.p.s.p.s delivered by each nerve branch revealed no significant differences ($0{\cdot}10 < P < 0{\cdot}20$ for both proximal and distal nerve branches; analysis based on two-tailed t test following arc sine transformation to normalize distribution of fractional e.p.s.p. values).

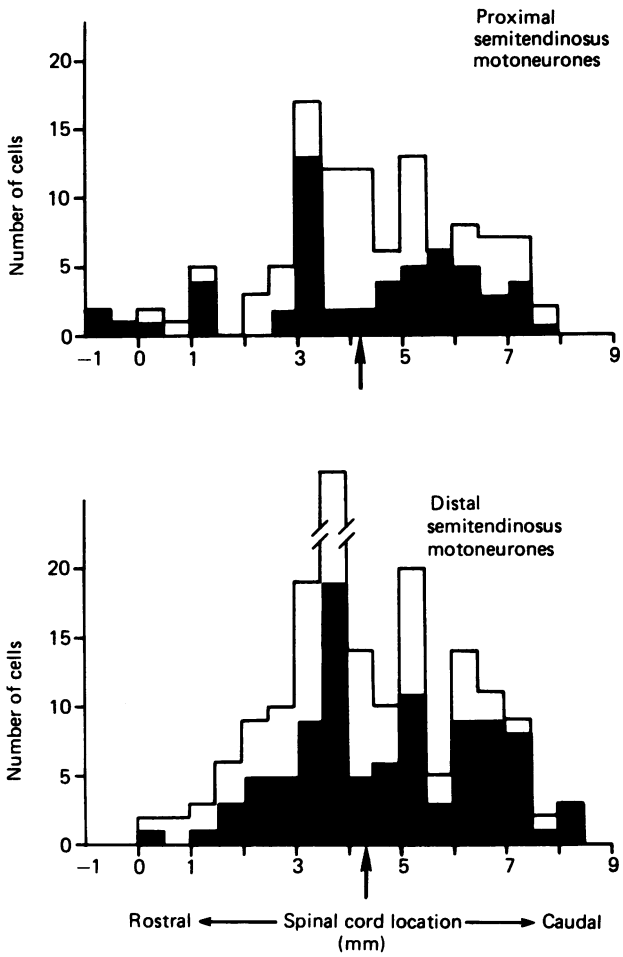

Fig. 4. Rostro-caudal location of semitendinosus motoneurones. This Figure presents histograms of cell locations relative to the L6–L7 dorsal root junction (marked '0'). Cells were identified in the process of intracellular recording by antidromic invasion in response to nerve branch stimulation. The larger population totals 283 cells from twenty-three experiments. The shaded areas represent the 151 cells from thirteen experiments from which e.p.s.p. data in this study were obtained. The arrows indicate the mean location of each cell group for the larger population of cells.

Topography in the semitendinosus motor nucleus

The absence of localized Ia projections to the semitendinosus motor nucleus suggested that this nucleus is not organized topographically. This issue was examined by comparing locations of proximal and distal semitendinosus motoneurones along the rostro-caudal axis of the spinal cord and by comparing the distribution of volleys elicited in the proximal and distal semitendinosus nerve branches by stimulation of the L6, L7 and S1 dorsal roots.

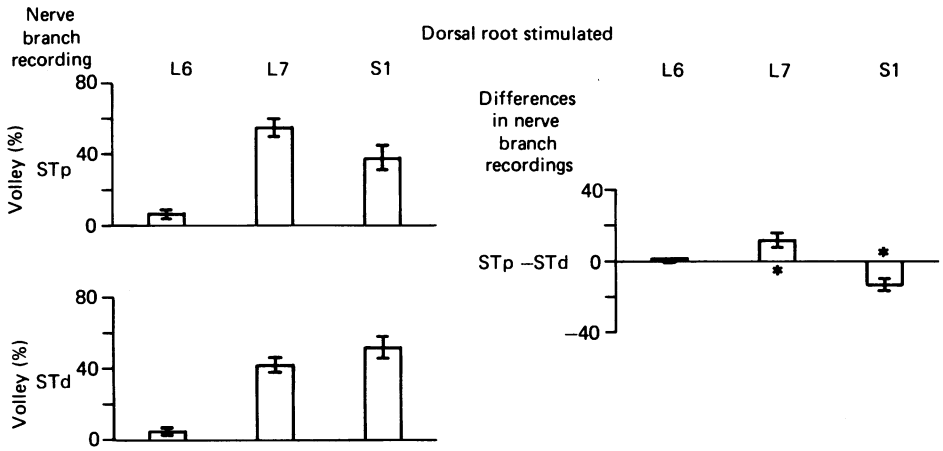

Fig. 5. Distribution of group I afferents in the dorsal roots. Maximum group I volleys were recorded in the proximal semitendinosus and distal semitendinosus nerve branches in response to stimulation of the sectioned L6, L7 and S1 dorsal roots at the end of each experiment. Each volley for a given nerve branch has been expressed as a percentage of the total for that branch (i.e. percent of L6 + L7 + S1 volleys.). The average values of these percent volleys (± S.E. of mean) are given in the left part of the Figure, which suggests that the group I volley of the proximal semitendinosus nerve branch is located in more rostral dorsal root segments than that of the distal semitendinosus nerve branch. This topographic organization is confirmed in the right part of the Figure. The averages (± S.E. of mean) of the differences between the percent volleys recorded in the proximal and distal semitendinosus nerve branches due to stimulation of each dorsal root division are plotted here. $*P < 0{\cdot}01$.

Fig. 4 shows histograms of the locations of proximal and distal semitendinosus motoneurones. The means for the two cell populations (4·17 mm caudal to the L6–L7 junction for proximal semitendinosus cells, 4·31 mm for distal semitendinosus cells) are nearly identical.

The possibility of a topographic arrangement of group I afferents from semitendinosus in the dorsal roots is examined in Fig. 5. The left half of Fig. 5 shows that proximal semitendinosus afferents tend to have more rostral positions in the dorsal roots than those from the distal compartments. This tendency is confirmed in the right half of Fig. 5, which summarizes comparisons of the volleys in the proximal and distal semitendinosus nerve branches on an experiment-by-experiment basis. This analysis, which compensates for the effects of variations in fixation of the motor nucleus, shows that proximal semitendinosus makes a larger relative contribution to

L7 than distal semitendinosus, while distal semitendinosus makes a larger relative contribution to S1.

The topographic arrangement of semitendinosus afferents demonstrated in Fig. 5 and the tendency of Ia afferents to produce larger e.p.s.p.s near their point of entry to the spinal cord than farther away (Lüscher, Ruenzel & Henneman, 1980) suggest

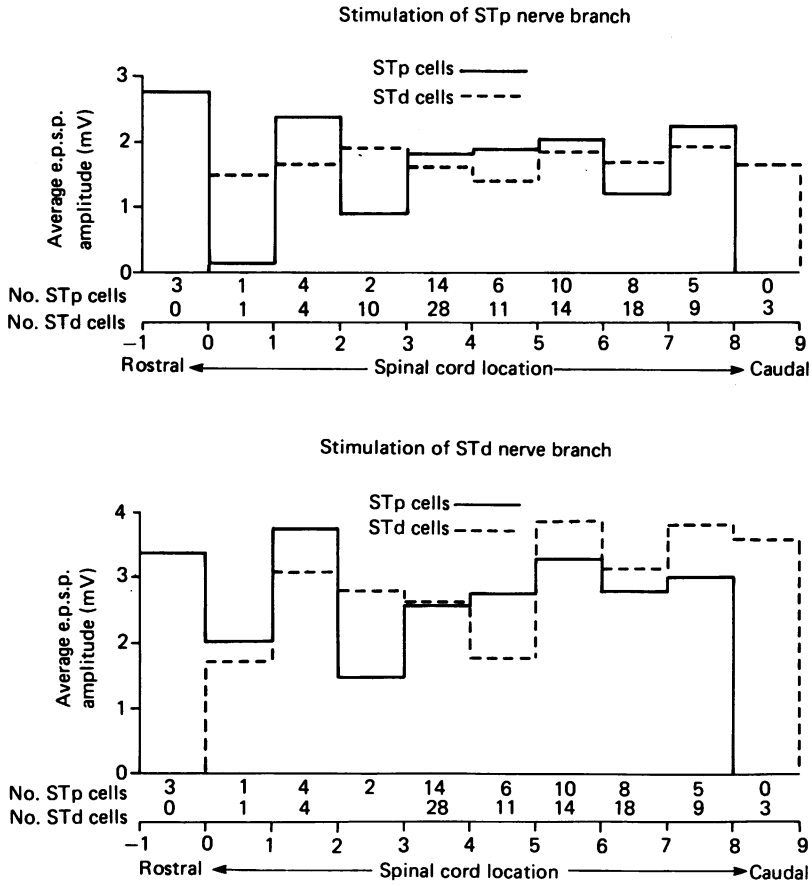

Fig. 6. Rostro-caudal distribution of e.p.s.p. amplitudes for proximal and distal semitendinosus motoneurones. Proximal and distal semitendinosus cells were grouped in 1 mm bins according to distance from the L6–L7 junction (marked '0' in the rostro-caudal direction). Within each bin average e.p.s.p. amplitudes in response to stimulation of the proximal semitendinosus nerve branch (top) and the distal semitendinosus branch (bottom) are plotted against location. The number of cells contributing to the average within each bin is indicated just above the axis marking location. Only a very slight tendency exists for e.p.s.p. amplitude to be dependent on cell location.

that e.p.s.p. amplitudes should have a dependence upon motoneurone location. This possibility is examined in Fig. 6, which shows that e.p.s.p. amplitude displays little dependence on motoneurone location in the spinal cord. This observation is supported by the results from performing polynomial regressions (through the cubic equation) between e.p.s.p. amplitude and cell location for each cell group. This analysis failed to demonstrate a dependence on cell location of e.p.s.p.s produced by the

semitendinosus nerve branches, except in the case of e.p.s.p.s produced in distal semitendinosus cells by the distal nerve branch. In this case, the optimal polynominal (quadratic) equation accounted for 7·9 % of the total variation in e.p.s.p. amplitude.

DISCUSSION

The present study demonstrates an absence of localized Ia projections to motoneurones supplying the in-series compartments of semitendinosus. This result is in contrast to that found in the motor nucleus of biceps femoris, in which localization has been demonstrated (Botterman *et al.* 1983). These results warrant discussion of the possible functional significance of the localization of Ia projections and of the roles that topography and neuronal recognition (Barondes, 1976) might play in the establishment of such connexions.

Significance of the localization of Ia e.p.s.p.s

Binder & Stuart (1980*b*) proposed that the strength of the synaptic effect on a motoneurone by a muscle receptor afferent is correlated with the strength of the mechanical coupling between the muscle receptor and the muscle unit of that motoneurone. This proposal originated from a number of observations (e.g. Binder, Kroin, Moore, Stauffer & Stuart, 1976; Binder & Stuart, 1980*a*; Cameron, Binder, Botterman, Reinking & Stuart, 1981; Windhorst, 1977; Windhorst & Meyer-Lohmann, 1977) which indicate that muscle receptors are preferentially sensitive to the contraction of neighbouring muscle units. Such a 'sensory partitioning' would provide a basis for a fine control of motoneuronal discharge, especially at low force levels, provided that a central correlate exists for the sensory partitioning. Our findings in the motor nuclei of biceps femoris and semitendinosus indicate that such localized control may exist in some motor nuclei but not in others and that the presence or absence of localization may depend upon characteristics of muscle structure and function. In this case, the localization of Ia projections would be another example in which Ia connexions are specialized to serve the needs of particular systems of motoneurones (summarized by Jankowska & Odutola, 1980).

The present study demonstrates that an inverse coupling (cf. Windhorst, 1978) exists between muscle spindles and motor units which are located in the two separate in-series compartments of semitendinosus in that a twitch contraction of one compartment produces a burst of spindle discharge from the other compartment rather than unloading (Fig. 2). Such inverse relations have also been observed due to contraction of single motor units in semitendinosus (Schwestka, Windhorst & Schaumberg, 1981). This pattern of spindle response is opposite to that which would be expected due to contraction of motor units positioned in-parallel to the receptor. Given this difference in the relation between spindle response and muscle activity between in-series and in-parallel muscle components, the finding of a difference in the organization of Ia connexions between motor nuclei whose muscles possess in-series and in-parallel structures is not surprising. Since in-series responses of muscle spindles can also be found in muscles not having strict in-series arrangements (Binder & Stuart, 1980*a*; Cameron *et al.* 1981), the degree and organization of localization in motor nuclei might depend in general upon the extent to which their muscles possess in-series or in-parallel arrangements.

The in-series arrangement of semitendinosus also has consequences for the effective development of force by this muscle. An in-series arrangement of motor units provides an example in which a great degree of synergy must be attained in order for efficient contraction to ensue, for in the case of separate activation, the visco-elasticity of the inactive component will result in marked shortening of the active component and a diminished and slowed twitch response. The inefficiency associated with a lack of synergy is demonstrated in the twitch forces of Fig. 2, which are markedly less during single-compartment contraction than during twitch of both in-series compartments (cf. Bodine, Roy, Meadows, Zernicke, Sacks, Fournier & Edgerton, 1982). Viewed from this perspective, the homogeneous distribution of monosynaptic Ia connexions throughout the semitendinosus motor nucleus is to be expected. It would tend to produce balanced activity of in-series motor units and, presumably, would be a characteristic of other incoming systems to the semitendinosus motor nucleus as well. Indeed, electromyograms recorded during locomotion in the cat display simultaneous activity in proximal semitendinosus and distal semitendinosus (Murphy, Roy & Bodine, 1981), although activity in the two compartments may be unequal (English & Letbetter, 1981).

Considering (i) the differences in muscle-receptor interactions between in-parallel and in-series muscle components; (ii) the need for unified activity in in-series muscle units while in-parallel units may operate effectively in independence, and (iii) the presence of a localization of Ia projections in the biceps femoris motor nucleus (Botterman *et al.* 1983) and its absence in the semitendinosus nucleus, it is suggested that Ia localization serves in the regulation of activity of divisions of a motoneurone pool whose muscle units may have somewhat varied actions. Accordingly, localized Ia projections might be expected in a motor nucleus when its muscle displays some diversity of action throughout its range of potential movements. This concept is an extension of the concept that Ia connectivity is related to muscle synergy put forward by Eccles, Eccles & Lundberg (1957). The localization of Ia projections departs from previous notions of the organization of motor nuclei, however, in the concept that there may exist some degree of diversity of action and control within a 'unifunctional' component of a motor nucleus–muscle complex. Aside from demonstrations of reflex localization (Bilotto, Schor, Uchino & Wilson, 1982; Cohen, 1953, 1954) and of localization of Ia e.p.s.p.s (Botterman *et al.* 1983; Brink *et al.* 1981; Lucas & Binder, 1981), evidence for such diversity exists in reports on two functional groups of motoneurones within the sartorius motor nucleus (Eccles & Lundberg, 1958; Hoffer, Loeb, O'Donovan & Pratt, 1980) and in a report of mutually exclusive connexions to motoneurones of the cat forelimb muscle extensor digitorum communis from two of its synergists (Fritz, Illert & Saggau, 1981). In addition, Desmedt & Godaux (1981) recently presented evidence demonstrating a re-ordering of the recruitment of motor units in human interosseus muscle when the recruitment order during voluntary flexion of the index finger was compared to that during abduction. Such evidence stresses a need for analysing motor control systems with respect to muscle action and movement rather than individual muscles.

Roles of topography and neuronal recognition in establishing localization

The absence of a significant topographic pattern of Ia connexions in the semitendinosus motor nucleus may be attributable to the organization of both the motoneurone and afferent systems. Our data on cell distributions in the semitendinosus and biceps femoris motor nuclei (present study and Botterman *et al.* 1983) are consistent with studies employing cell labelling with horseradish peroxidase (Letbetter & English, 1981), which demonstrate nearly complete overlap of the proximal semitendinosus and distal semitendinosus cell groups, except at the extremes of the nucleus, while anterior, middle and posterior biceps cell groups, though showing considerable overlap, are separable to a greater extent. Thus, the absence and presence of localized Ia projections in these two motor nuclei find some correspondence in the extent of overlap of the different groups of motoneurones. Furthermore, despite the semitendinosus group I afferents having preferred areas of entry to the spinal cord, e.p.s.p. amplitudes display little dependence upon motoneurone location. This independence of cell location suggests that Ia afferents distribute their connexions homogeneously throughout the motor nucleus of semitendinosus, in apparent contrast to those of biceps femoris, in which motor nucleus a dependence of e.p.s.p. amplitude on cell location is evident (Botterman *et al.* 1983). It appears, then, that the afferent topography of semitendinosus is subordinated to other factors in determining e.p.s.p. amplitudes. Considering also the importance of neuronal recognition in determing Ia connexions in the motor nucleus of biceps femoris (Botterman *et al.* 1983), we suggest that while topographic factors may be of importance in establishing a basis for the pattern of Ia connexions, neuronal recognition is important in determining the ultimate pattern of Ia connectivity in a motor nucleus appropriate for its role in neuromuscular function.

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