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PARTITIONING OF MONOSYNAPTIC Ia EXCITATORY POST-SYNAPTIC POTENTIALS IN THE MOTOR NUCLEUS OF THE CAT SEMIMEMBRANOSUS MUSCLE

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SUMMARY

1. In anaesthetized low-spinal cats, intracellular recordings were made of the Ia excitatory post-synaptic potential (e.p.s.p.) responses of semimembranosus motoneurones to electrical stimulation (Group I range) of nerve branches supplying the anterior and posterior heads of semimembranosus, the anterior and posterior parts of biceps femoris, and the distal part of semitendinosus. Recordings were also made during stimulation of nerves to the gracilis muscle and to the vasti muscle group.

2. Stimulation of the semimembranosus-anterior nerve branch produced Ia e.p.s.p.s of greater amplitude in semimembranosus-anterior motoneurones than in semimembranosus-posterior cells; likewise, stimulation of the semimembranosus-posterior nerve branch produced larger e.p.s.p.s in cells which supplied the posterior head than in those which supplied the anterior head.

3. Stimulation of the nerve branches to components of two 'flexor' muscles (Sherrington, 1910), biceps-posterior and semitendinosus-distal, produced larger e.p.s.p.s in semimembranosus-posterior cells than in the anterior motoneurones. A tendency was found for stimulation of the nerve to biceps femoris-anterior (an 'extensor') to produce larger e.p.s.p.s in semimembranosus-anterior than in -posterior motoneurones. However, this effect was of borderline ($0{\cdot}06 > P > 0{\cdot}05$) significance. The limited monosynaptic input produced by stimulation of the nerves to the gracilis and vasti muscles showed that their Ia axons do not distinguish between the two semimembranosus cell groups.

4. A slight topographic organization of motoneurones within the semimembranosus motor nucleus was found, with anterior cells encountered, on average, at a more rostral level of the spinal cord than posterior cells. A similar topographic arrangement was observed in the rostrocaudal distribution of Group I afferent fibres in the dorsal roots and motor axons from the two sets of motoneurones in the ventral roots. These findings are consistent with 'location specificity' (Scott & Mendell, 1976) being a factor which contributes to the observed pattern of homonymous Ia connexions.

5. A role for 'species specificity' (Scott & Mendell, 1976) in determining the

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observed pattern of homonymous Ia connexions was indicated by species-dependent differences in e.p.s.p. amplitude in pairs of semimembranosus-anterior and -posterior motoneurones at similar rostrocaudal locations in the spinal cord.

6. The pattern of heteronymous connexions to the semimembranosus motor nucleus also showed evidence for species specificity. However, no clear topographic pattern was evident in these connexions.

INTRODUCTION

Recently, 'partitioning' of Ia excitatory post-synaptic potentials (e.p.s.p.s) has been demonstrated in five motor nuclei of the cat spinal cord (splenius and biventer cervicis: Brink, Jinnai & Wilson, 1981; biceps femoris: Botterman, Hamm, Reinking & Stuart, 1983*a*; medial gastrocnemius: Lucas & Binder, 1984; Lucas, Cope & Binder, 1984; lateral gastrocnemius: Vanden Noven, Hamm & Stuart, 1983, 1984). In this context, partitioning means that spindle Ia afferents from the homonymous muscle make more effective connexions (as determined by differing amplitudes of e.p.s.p.s) with their 'own' motoneurones (i.e. those that supply the same region of the muscle in which the afferents' receptors are located), than with motoneurones supplying other regions of the muscle (see also, Munson, Fleshman, Zengel & Sypert, 1984).

Recent reports from this laboratory used the term 'localization' as a synonym for 'partitioning' (Botterman, Hamm, Reinking & Stuart, 1983*a*, *b*; Vanden Noven, Koehler, Hamm & Stuart, 1983; Vanden Noven, Hamm & Stuart, 1983, 1984). However, in the present report, localization is discarded because it implies a mechanism (i.e. 'location specificity' as defined below) which may or may not contribute to the presence of partitioned e.p.s.p.s.

The above findings on partitioned e.p.s.p.s are consistent with others on the presence of an intramuscular localization of the stretch reflex in three cat muscles (rectus femoris and vastus intermedius: Cohen, 1953, 1954; splenius: Bilotto, Schor, Uchino & Wilson, 1982; Ezure, Fukushima, Schor & Wilson, 1983).

At least one spinal motor nucleus supplying the cat hind-limb muscle, semitendinosus (Nelson & Mendell, 1978; Botterman *et al.* 1983*b*), does not exhibit a partitioning of Ia e.p.s.p.s. The semitendinosus muscle has two muscle compartments combined in an atypical in-series arrangement. Perhaps partitioning is absent in the motor nucleus because the muscle would be at a functional disadvantage if a dissociation of intramuscular actions were to occur (Botterman *et al.* 1983*b*). Indeed, neither compartment of the semitendinosus muscle has been reported capable of independent activity (Murphy, Roy & Bodine, 1981). For a similar reason, there may be no intramuscular localization of short-latency (including the Ia pathway) proprioceptive reflex effects in the human tibialis anterior muscle (McKeon, Gandevia & Burke, 1984; see also Smith, Pratt & Moore, 1983).

These various results have prompted us to consider the possibility that a partitioning of Ia e.p.s.p.s is present in motor nuclei supplying muscles with regions capable of independent and different actions (viz. biceps femoris: Botterman *et al.* 1983*a*). For a candidate to test this possibility, we chose the cat semimembranosus muscle, a hind-limb muscle which takes origin from the tuberosity of the ischium.

The semimembranosus muscle has two heads (Peters & Rick, 1977): an anterior

one which attaches to the distal femur and a posterior one connecting to the proximal tibia. Each head has been shown to have somewhat different actions during stepping (Engberg & Lundberg, 1969) but, in contrast to the prediction from our hypothesis, Eccles & Lundberg (1958) reported no significant differences in the Ia distribution (i.e. amplitudes of Ia e.p.s.p.s in motoneurones when stimulating homonymous and heteronymous nerve branches) between the two heads.

However, in the present investigation, evidence has been found for partitioning of Ia projections between the anterior and posterior cell groups within the semimembranosus motor nucleus. In addition, data have been gathered regarding the relative contributions of 'location specificity' and 'species specificity' to this partitioning (Scott & Mendell, 1976; Lüscher, Ruenzel & Henneman, 1980). For the present purposes, location specificity is defined as an arrangement in which the efficacy of excitatory monosynaptic connexions between the central projections of spindle Ia afferents and their target motoneurones is attributable to the anatomical proximity of the afferent's entry point and motoneurone location within the spinal cord. Species specificity, on the other hand, is an arrangement in which this efficacy is independent of topographic relationships within the spinal cord and is dependent, rather, on the anatomical proximity of the peripheral terminations of the sensory and motor axons within the muscle.

A preliminary account has been presented (Vanden Noven, Koehler, Hamm & Stuart, 1983).

METHODS

Preparation

Adult cats (2·5–4·0 kg) were anaesthetized for initial surgical procedures with halothane, nitrous oxide and oxygen. A mixture of α-chloralose (60 mg/kg) and urethane (600 mg/kg) was given intravenously during preparation of the hind limb and subsequent recording. This anaesthetic mixture produced a deep anaesthesia which was sustained by giving additional doses (at one-fifth the original strength) as needed throughout the experiment. For recording, the animal was mounted in a Göteborg-type frame. Upon occasion, the animal was paralysed by the intravenous administration of gallamine triethiodide and artificially respired, in order to stabilize the spinal cord for more secure intracellular recording from motoneurones.

Selected muscle nerves were cut and subsequently mounted on bipolar stimulating electrodes. For the test muscle, semimembranosus, the dissection involved the detachment and reflexion of the biceps femoris from its insertion to expose the nerve branches to semimembranosus, semitendinosus and biceps femoris (Fig. 1). The semimembranosus nerve was separated into its two primary nerve branches: semimembranosus-anterior which innervates the anterior (femoral) head and semimembranosus-posterior supplying the posterior (tibial) head.

Heteronymous nerve branches prepared for stimulation included those supplying the anterior and posterior parts of biceps femoris and the distal part of semitendinosus. The nerve branch innervating the middle part of biceps femoris was removed from the main innervation of the muscle in order to eliminate results due to mixed effects (Botterman *et al.* 1983*a*). The micro-electrode search for semimembranosus motoneurones within the spinal cord was facilitated by also preparing for stimulation the nerves to gastrocnemius–soleus, the tibial and the common peroneal nerves. In addition, two nerves supplying ventral musculature of the thigh, the gracilis muscle and the vasti muscles (i.e. vastus lateralis, medialis and intermedius), were cut and placed in nerve cuff electrodes for subsequent stimulation.

The nerve cuff electrodes (cf. Stein, Nichols, Jhamandas, Davis & Charles, 1977; Barone & Wayner, 1979) consisted of a Silastic tube with two internal bare wire coils. The two 25 cm wires protruding from the tube were insulated, twisted and attached to electrical connectors. The cut

end of the nerve was tied and pulled through the tube with a straight needle. The cuff electrode was secured to an adjacent muscle with thread ties. Petroleum jelly was injected into the tube to force out any fluid and to 'seal' the nerve cuff.

The spinal cord was transected at the T12–L1 level and the lumbosacral cord exposed by laminectomy. Paraffin oil pools were formed at the cord and leg by drawing up skin flaps. The biceps femoris, semitendinosus and semimembranosus-posterior muscles were removed to provide space in the leg bath for the stimulating electrodes. Rectal and leg pool temperatures were controlled separately at 37 ± 1 °C (Watt, Stauffer, Taylor, Reinking & Stuart, 1976).

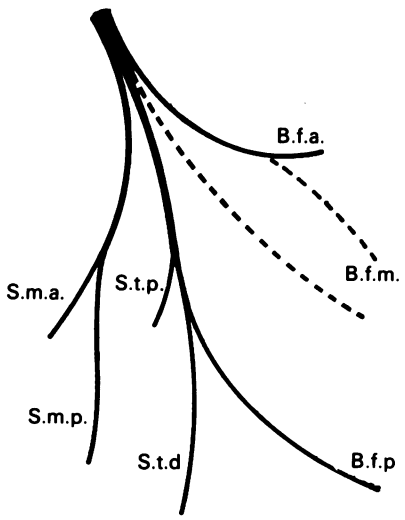

Fig. 1. Hamstring innervation. A schematic view of the innervation of the hamstring muscles, as viewed by reflecting the antero-lateral border of biceps femoris to expose its innermost surface and the dorsal surfaces of semimembranosus and semitendinosus. Common features of hamstring innervation include: nerve branches to the anterior (b.f.a.) and posterior (b.f.p.) parts of biceps femoris; a nerve to semimembranosus which divides to innervate its anterior (s.m.a.) and posterior (s.m.p.) parts; and nerve branches to the proximal (s.t.p.) and distal (s.t.d.) compartments of semitendinosus (Chin, Cope & Pang, 1962). The middle (b.f.m.) part of biceps femoris (indicated by dashed lines) may be innervated by a deep nerve branch that divides from the branch to b.f.a. or by a separate branch that divides from a more distal level of the hamstring nerve trunk. The same abbreviations are used in subsequent Figures.

Recording procedures

Dorsal root volleys produced by stimulation of the test nerves or branches were recorded with a monopolar stainless-steel electrode placed under the L6–S1 dorsal roots. An indifferent electrode was placed in the back musculature.

Intracellular potentials were recorded from motoneurones using glass micro-electrodes filled with 2 M-potassium citrate. The tips of these electrodes were broken to 1–1·5 μm and bevelled (Botterman *et al.* 1983*a*) to a final impedance of 3–5 MΩ.

Motoneurones were identified as supplying the semimembranosus-anterior or -posterior muscle head on the basis of their antidromic invasion from stimulation of one or the other of the two semimembranosus nerve branches. Motoneurones were accepted for study if their 'resting' potentials were at least 50 mV. Once impalement was secure, e.p.s.p.s were elicited by stimulation of the test muscle nerve branches using 0·1 ms stimulus pulses at a rate of 2 Hz. Stimulus strengths were graded to achieve the maximum Ia e.p.s.p. (approximately 2 × threshold).

If a cell was activated antidromically before the attainment of a maximum Ia e.p.s.p., 50 ms pulses of hyperpolarizing current were injected through the electrode at sufficient intensity to block the antidromic action potential, leaving the e.p.s.p. superimposed on an M spike (Hamm, Botterman, Reinking & Stuart, 1983).

Measurements were also made of rheobase (technique of Fleshman, Munson, Sypert & Friedman, 1981) and input resistance (e.g. Barrett & Crill, 1974). These measurements were accepted as indicators of the cell's intrinsic properties in the absence of severe electrode polarization and if the resting potential remained at least 50 mV during the tests.

TABLE 1. Intrinsic characteristics of semimembranosus motoneurones

	Cell group	
	Semimembranosus-anterior motoneurones	Semimembranosus-posterior motoneurones
Resting potential (mV)	62·5 ± 1·0 (86)	62·0 ± 0·83 (76)
Input resistance (MΩ)	0·59 ± 0·05 (40)	0·57 ± 0·05 (42)
Rheobase (nA)	15·09 ± 1·33 (40)	13·51 ± 1·21 (44)
Rheobase/input resistance (nA/MΩ)	33·01 ± 3·69 (40)	47·69 ± 10·34 (42)

Values expressed as mean ± S.E. of mean (with number of cells in parentheses).

The locations of the test motoneurones within the spinal cord were plotted, as well as the distribution of volleys produced in each nerve branch by stimulation of the dorsal and ventral roots. Motoneurone positions along the rostrocaudal axis of the spinal cord were noted relative to a reference point at the L6–L7 dorsal-root junction (Stauffer & Watt, 1976). At the end of each experiment, the L5–S1 dorsal and ventral roots were sectioned and individually put up on a stimulating electrode. Each root was stimulated to produce a maximal Group I volley while recording sequentially from the two nerve branches to semimembranosus. This procedure provided information on the distribution of Group I afferents and efferents in each nerve branch to the various dorsal and ventral roots, respectively.

Data analysis

Several wave forms were stored concurrently on FM tape for off-line analysis using a signal averager and small laboratory computer. They included: high-gain e.p.s.p.s (sixteen samples), dorsal root volleys, low-gain motoneurone potentials and the amount of current passed into the cell for various tests.

To correct an e.p.s.p. record containing an M spike so as to account for the contribution of the spike, an 'average' M spike was subtracted from each homonymous 'M+e.p.s.p.' record (Hamm *et al.* 1983). The average M spike was obtained from fifty-two semimembranosus motoneurones in control preparations with sectioned dorsal roots.

RESULTS

Intrinsic properties of semimembranosus motoneurones

Ia e.p.s.p. amplitude has been shown to be dependent, to some extent, on motoneurone 'type', increasing in the order FF, FR, S (nomenclature of Burke, Levine, Tsairis & Zajac, 1973; see also Burke, 1981). Therefore, any difference in mean e.p.s.p. amplitude between the two semimembranosus motoneurone groups could be attributed to significant differences in the numbers of type FF, FR and S cells within each group. Consequently, it was necessary to estimate whether the two semimembranosus cell groups were similar with respect to the different motoneurone types.

In Munson's laboratory, rheobase and input resistance values have been found to provide an indirect estimate of the different motoneurone types in barbiturate-anaesthetized cats (Fleshman *et al.* 1981). Rheobase values > 10 nA were found predominantly in type F (i.e. FF + FI + FR) cells, whereas those < 5 nA were found in type S. In addition, the division of rheobase by input resistance (nA/MΩ; Zengel,

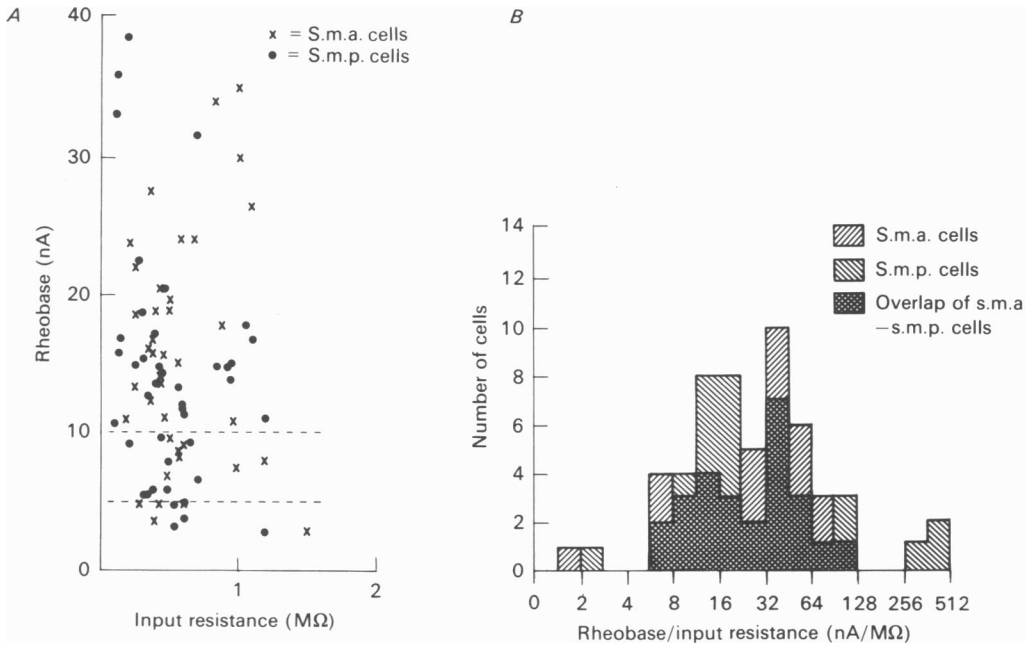

Fig. 2. Distribution of input resistance and rheobase values for semimembranosus motoneurones. *A*, scatter plot of rheobase *versus* input resistance for the present sample of semimembranosus motoneurones ($n = 82$). Values below the lower dashed line represent presumed type S motoneurones (cf. Fleshman *et al.* 1981), whereas those above the upper line represent putative type F cells. *B*, distribution of rheobase/input resistance ratios for semimembranosus motoneurones. Data plotted on a $\log_2$ scale to provide suitable display for this multiplicative relationship. This ratio provides approximate divisions between type S (0–7), type FR (7–18) and type FF (18) motoneurones (cf. Zengel *et al.* 1985). Both plots suggest that the present semimembranosus cell population consists of primarily type F (large) motoneurones.

Reid, Sypert & Munson, 1985) provided an index for separation of the different motoneurone types with FF > 18 > FR > 7 > S.

For our present sample of semimembranosus motoneurones, measurents were made of rheobase and input resistance and the ratio of rheobase/input resistance calculated in order to compare the distribution of these values for the semimembranosus-anterior and -posterior cell groups. As shown in Table 1, the mean values of these variables were not found to be significantly different between the two semimembranosus populations.

In Fig. 2*A* the distributions of rheobase and input resistance values are plotted for the two semimembranosus cell groups. The similarity of the two distributions suggests that the two cell populations had similar compositions with respect to

motor-unit type. The values of rheobase suggest that the majority of motoneurones in both groups were type F (FF + FR), with type S motoneurones being represented minimally (*ca.* 12·5%). Likewise in Fig. 2*B*, the distribution of rheobase/input resistance ratios is plotted. Again, the two distributions are similar (Table 1) and suggest a predominance of type F motoneurones.

This separation of semimembranosus motoneurones into the different motoneurone types by rheobase is only a rough estimate since these values in chloralose-anaesthetized cats may not be comparable (Powers, 1982) to the medial gastrocnemius values of Fleshman *et al.* (1981) and Zengel *et al.* (1985). However, the estimated separation is in keeping with the histochemial study of Ariano, Armstrong & Edgerton (1973) of fibre-type distributions within the two heads of the semimembranosus muscle. Semimembranosus-anterior was reported to show only 10% SO fibres; likewise, semimembranosus-posterior had 9% SO fibres. Such a small percentage of SO fibres suggests far fewer type S than type F motoneurones, since the innervation ratio of type S motor units in cat hind-limb muscles can be anticipated to be similar to that of type FR units and somewhat smaller than that of type FF units (for review see McDonagh, Binder, Reinking & Stuart, 1980; Burke, 1981).

Alternatively, Hultborn & Katz (1983) have used the product of rheobase and input resistance of medial gastrocnemius motoneurones (also barbiturate anaesthesia) as an indirect measure of firing threshold (i.e. nA × MΩ = mV) and showed that, in their sample, it increased in the order of S, FR, FF with mean values of 4·6, 8·9 and 13·5 mV, respectively. However, this second procedure led to ambiguous results (J. Munson, personal communication) when applied to the type-identified population of medial gastrocnemius motoneurones from the studies of Fleshman *et al.* (1981) and Zengel *et al.* (1985).

Homonymous Ia e.p.s.p.s

Fig. 3 gives examples of Ia e.p.s.p.s in both an individual semimembranosus-anterior and -posterior motoneurones due to stimulation of the nerve branches supplying the two heads of the semimembranosus muscle. The 'own-branch' e.p.s.p.s have been corrected for the presence of an M spike. As shown here, the own-branch e.p.s.p.s were often larger than the 'other-branch' ones, in contrast with the earlier findings of Eccles & Lundberg (1958). These differences were significant when the full sample was compared (Table 2). Each cell exhibited an e.p.s.p. from stimulation of its own nerve branch, and most cells (94%) responded with an e.p.s.p. to stimulation of the other branch.

The degree of partitioning was similar for the input from both nerve branches as judged by the similar magnitudes of the differences between own-branch and other-branch e.p.s.p. values in the two cell groups (0·34 and 0·30 mV for stimulation of semimembranosus-anterior and -posterior nerve branches, respectively). Likewise, the sums of own-branch and other-branch e.p.s.p.s were quite similar (1·30 and 1·26 mV, respectively). The two comparisons suggest no asymmetries in the synaptic input received by each cell group, a feature consistent with a similar distribution of motoneurone types in the two cell groups. Consequently, the normalization used by Botterman *et al.* (1983*a*) was not employed in this study.

Heteronymous Ia e.p.s.p.s

Table 3 shows evidence for a partitioning of heteronymous Ia e.p.s.p.s in at least two of the five tested pathways. The majority of semimembranosus motoneurones received inputs from the heteronymous hamstring-nerve branches. Stimulation of the nerve branches to biceps femoris-posterior and semitendinosus-distal produced significantly larger e.p.s.p.s in semimembranosus-posterior motoneurones than in the

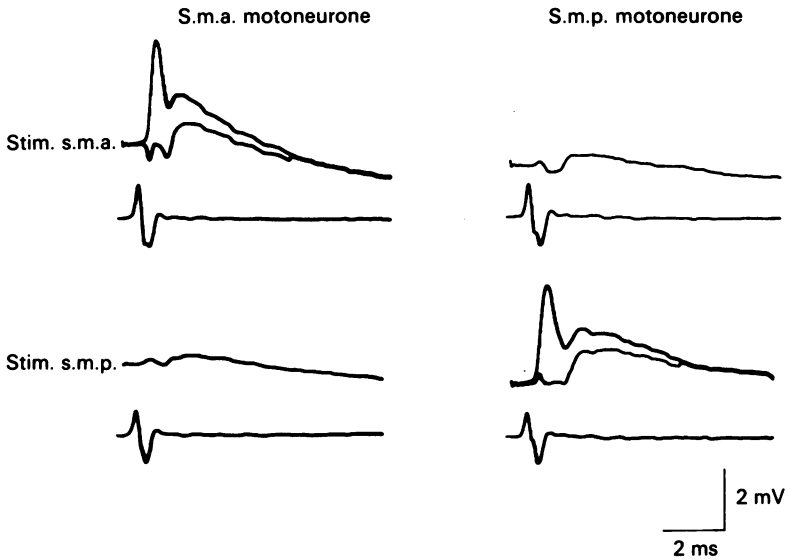

Fig. 3. Composite homonymous e.p.s.p.s recorded in semimembranosus-anterior and -posterior motoneurones. E.p.s.p.s produced by stimulation of the semimembranosus-anterior and -posterior nerve branches are displayed in an individual semimembranosus-anterior cell (left) and -posterior cell (right). Below each intracellular trace is the dorsal-root recording. For own-branch e.p.s.p.s, hyperpolarizing current was injected, as necessary, into the cells to block the response to the 'M spike+e.p.s.p.'. The original records are distinguished by the initial M spike, while the records which have been corrected for the M spike are superimposed. A tendency can be seen for the own-branch e.p.s.p.s to be the largest.

anterior cells. In addition, stimulation of the nerve branch to biceps femoris-anterior produced larger e.p.s.p.s in the semimembranosus-anterior than -posterior motoneurones. However, this effect proved to be of borderline significance ($0{\cdot}05 < P < 0{\cdot}06$; two-tailed Student's t test). The limited number of monosynaptic e.p.s.p. responses observed upon stimulation of the nerves to gracilis and vasti showed no significant partitioning of input to the two cell groups in the semimembranosus motor nucleus.

Location and species specificity in the semimembranosus motor nucleus

Evidence for the contributions of location and species specificity to the observed partitioning of Ia e.p.s.p.s was sought in the topographic organization of semimembranosus motoneurones and Group I afferents as well as in the dependence of

e.p.s.p. amplitude on motoneurone location and species. If location specificity governed the establishment of Ia motoneuronal connexions, then motoneurones in close proximity to the afferents' entry points would receive the strongest connexions (Lüscher *et al.* 1980). In the present case, a partitioning of Ia e.p.s.p.s would result if semimembranosus-anterior and -posterior motoneurones had different mean

TABLE 2. Amplitudes of mean composite monosynaptic Ia e.p.s.p.s evoked by stimulation of homonymous nerve branches from semimembranosus

	Cell group		
Nerve branch stimulated	Semimembranosus-anterior motoneurones	Semimembranosus-posterior motoneurones	Difference
Semimembranosus-anterior	0·79 ± 0·07 (86/86)**	0·45 ± 0·05 (76/76)	0·34
Semimembranosus-posterior	0·51 ± 0·04 (82/86)**	0·81 ± 0·05 (76/76)	0·30
Sum	1·30	1·26	

E.p.s.p. values (mV) expressed as mean ± S.E. of mean (with number of observed e.p.s.p.s/total number of cells examined in parentheses). Comparisons should be limited to the effects of a given nerve branch on the two cell groups to avoid any differences in amplitude due to a variable number of afferents between the nerve branches. Asterisks indicate significant differences between adjacent e.p.s.p. averages in each row (** $P < 0·001$; two-tailed Student's t test).

TABLE 3. Amplitudes of mean composite monosynaptic Ia e.p.s.p.s evoked by stimulation of heteronymous inputs to semimembranosus motoneurones

	Cell group	
Nerve/branch stimulated	Semimembranosus-anterior motoneurones	Semimembranosus-posterior motoneurones
Biceps femoris-anterior	0·27 ± 0·02 (70/73)	0·21 ± 0·02 (65/72)
Biceps femoris-posterior	0·25 ± 0·03 (65/72)*	0·38 ± 0·04 (59/69)
Semitendinosus-distal	0·28 ± 0·04 (60/74)**	0·74 ± 0·07 (66/73)
Gracilis	0·08 ± 0·03 (10/29)	0·12 ± 0·04 (8/19)
Vasti	0·17 ± 0·04 (19/42)	0·10 ± 0·05 (5/34)

E.p.s.p.s (mV) expressed as mean ± S.E. of mean (with number of observed e.p.s.p.s/total number of cells examined in parentheses). Comparisons are limited to the effects of each nerve branch on the two cell groups to avoid differences in the number of afferents between nerve branches. Asterisks indicate significant differences between adjacent e.p.s.p. averages in each row (* $P < 0·02$; ** $P < 0·001$; two-tailed Student's t test).

locations corresponding to different mean afferent entry points of their respective Ia afferents. However, e.p.s.p. amplitude could conceivably be independent of the relative topography between afferents and motoneurones. Therefore, a topographic organization is a necessary but not sufficient condition for location specificity. In contrast, if species specificity dictated the development of Ia motoneuronal connexions, the test afferents would show preferential connectivity (i.e. greater amplitude of e.p.s.p.s) with their own homonymous-branch motoneurones in com-

parison to connectivity with other homonymous-branch motoneurones, regardless of the relative locations of motoneurones and afferents.

Homonymous connexions. A topographic organization was observed in the semimembranosus motor nucleus and corresponding dorsal and ventral roots. Fig. 4 shows the locations of semimembranosus-anterior and -posterior motoneurones relative to

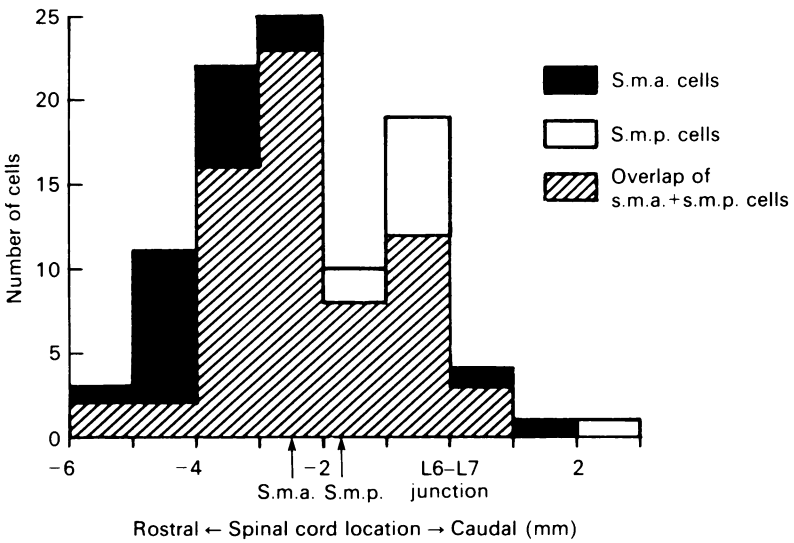

Fig. 4. Spinal-cord location of semimembranosus motoneurones. Histograms show rostro-caudal locations relative to the L6–L7 dorsal root junction (with arrows at mean location of the semimembranosus-anterior and -posterior cell groups). The semimembranosus population totalled 162 cells from nine experiments (86 anterior and 76 posterior cells). On average, the semimembranosus-anterior cells were slightly more rostral than the -posterior cells ($P < 0{\cdot}02$, Student's t test).

the junction of the L6–L7 dorsal roots. Despite extensive overlap of these two cell groups, the mean locations (arrows) were significantly different ($P < 0{\cdot}02$; Student's t test) with the mean of the semimembranosus-anterior population slightly more rostral than that of the semimembranosus-posterior population. This tendency was also found in the cell location data from single experiments.

Fig. 5. Topography of axonal connexions between the spinal cord and the semimembranosus muscle. Maximum Group I (afferent) and α axon (efferent) volleys were recorded in semimembranosus-anterior and -posterior nerve branches in response to stimulation of sectioned L5, L6, L7 and S1 dorsal and ventral roots, respectively. The volley for each branch was expressed as a percentage of the total for that nerve branch (i.e. a percentage of L5 + L6 + L7 + S1 volleys). On the left, the average values (± S.E. of mean) of the percent volleys produced in the semimembranosus-anterior and -posterior nerve branches by stimulation of each root are shown. These data show that semimembranosus-anterior had a stronger representation than semimembranosus-posterior in the L6 dorsal and ventral roots, the reverse occurring in the L7 roots. This topographic organization is confirmed in the right-hand part of the Figure. Plotted here are the averages (± S.E. of mean) of the differences between the percent volleys recorded in the anterior and posterior semimembranosus nerve branches in each experiment due to stimulation of each dorsal and ventral root division (* $P < 0{\cdot}05$).

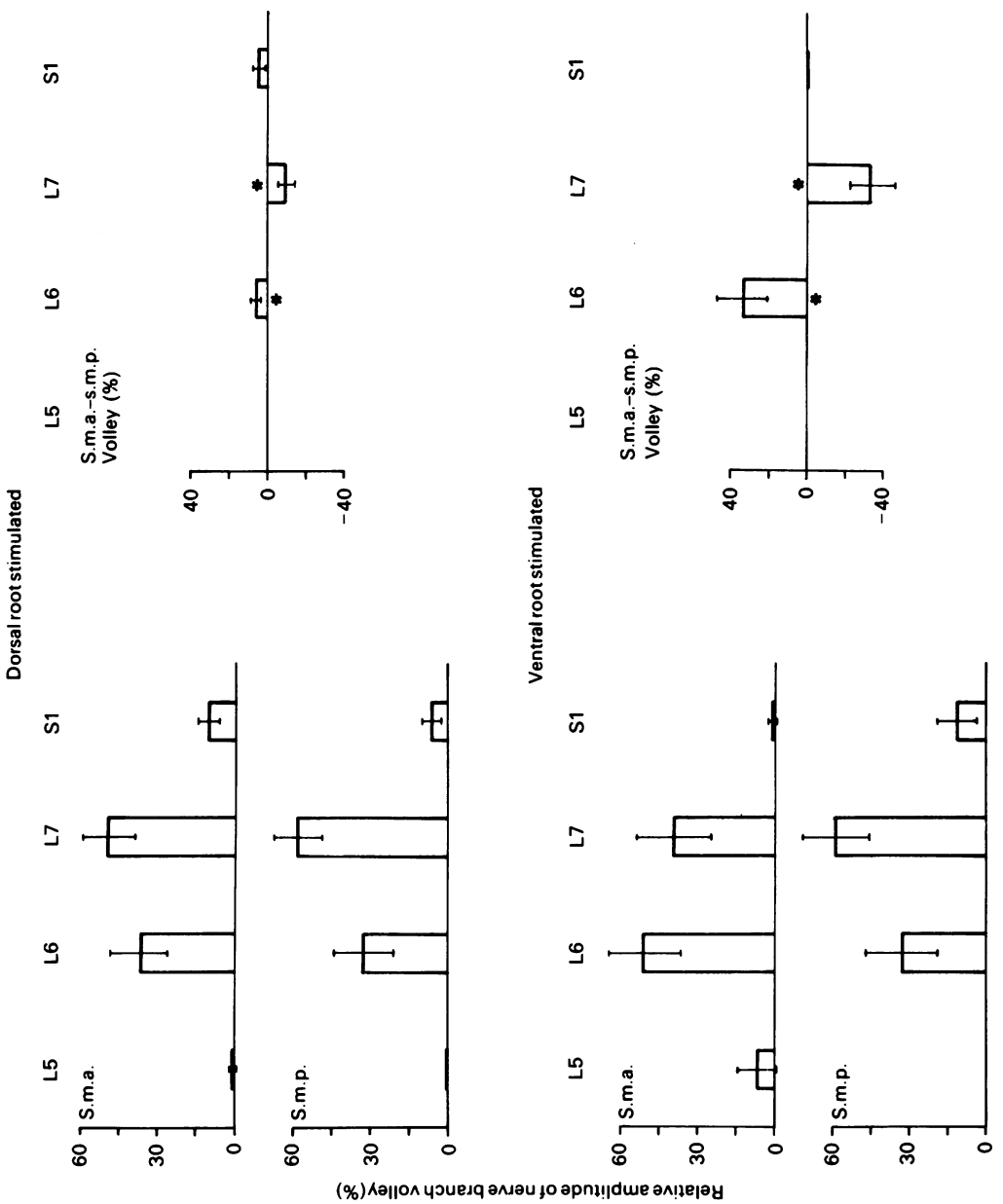

Fig. 5. For legend see opposite.

Evidence for a topographic organization of Group I and α-motor fibres is demonstrated in Fig. 5, which shows the points of entry or exit of these fibres within the dorsal and ventral roots, respectively. In Fig. 5 (left-hand side), a distinct topographic organization is evident in the ventral roots. A larger percentage of the semimembranosus-anterior motor axons were found in the more rostral roots (primarily L6), whereas a greater percentage of semimembranosus-posterior axons were found in the more caudal roots (primarily L7). This finding is consistent with the more rostral location of semimembranosus-anterior cells in the semimembranosus motor nucleus. A similar, though less distinct, topographic organization was found in the dorsal roots.

Differences in the distribution of the afferents and efferents were tested for statistical significance by taking pairwise differences in the amplitudes of the volleys produced in the semimembranosus-anterior and -posterior nerve branches by stimulation of each dorsal or ventral root segment in each experiment. In both dorsal and ventral roots (Fig. 5, right-hand side) the semimembranosus-anterior nerve branch received a larger percentage of its volley from the L6 root than semimembranosus-posterior did, while semimembranosus-posterior's L7 volley was a greater part of its total than was semimembranosus-anterior's L7 volley. In averaging these pairwise differences, data were excluded from two cats: one whose lumbosacral cord was markedly pre-fixed and one with a post-fixed cord (Romanes, 1951); however, the trend was the same in these two as in the larger sample.

The preceding results demonstrate the existence of a slight topographic organization in the semimembranosus motor nucleus. However, our data indicate that species specificity contributes prominently to the partitioning of Ia projections.

Fig. 6 shows that along the length of the motor nucleus the semimembranosus-anterior nerve branch (top) produced larger e.p.s.p.s in the semimembranosus-anterior cells as compared with those from posterior cells. Likewise, the semimembranosus-posterior nerve branch (bottom) produced larger e.p.s.p.s in the semimembranosus-posterior cells throughout most of the nucleus.

As shown in Fig. 7*A*, potential effects due to location specificity were minimized by examining the difference between the e.p.s.p.s produced upon stimulation of the semimembranosus-anterior (or -posterior) nerve branch in pairs of motoneurones (semimembranosus-anterior and -posterior) located within 0·5 mm of each other. Each semimembranosus nerve branch appeared to 'recognize' its own cell preferentially over the other-branch cell, which supports a role for species specificity in determining the pattern of homonymous Ia projections.

In making these comparisons, the pairs were selected with certain restrictions: (1) no single cell was included in more than three pairs and (2) a cell pair was not accepted if the difference in input resistance of the cells was greater than 0·3 MΩ (the average difference between type FF and FR motoneurones, at least for cells supplying the medial gastrocnemius muscle: Fleshman *et al.* 1981).

Results in Fig. 7*A* are consistent with the differences found in Table 2. Although the difference in the effects of the semimembranosus-anterior nerve branch on semimembranosus-anterior and -posterior cells was not significant, the e.p.s.p. amplitudes still tended to be larger in the anterior cells ($0{\cdot}05 < P < 0{\cdot}1$). According

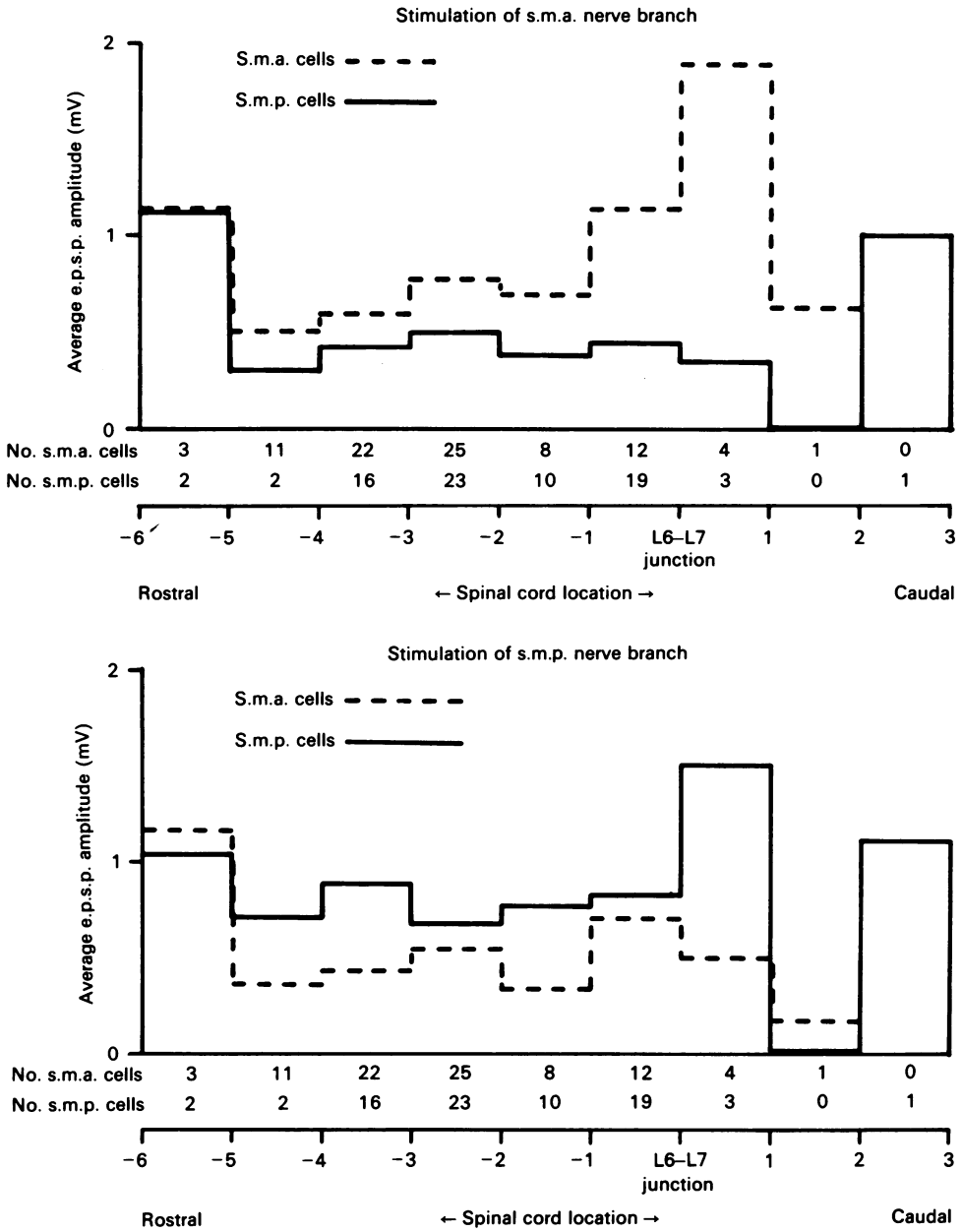

Fig. 6. Relationship between e.p.s.p. amplitude and spinal cord location of the tested semimembranosus cells. Bar graphs show rostrocaudal distributions of homonymous e.p.s.p. amplitudes for semimembranosus-anterior and -posterior motoneurones. Semimembranosus-anterior and -posterior cells were grouped in 1 mm bins according to their rostrocaudal distance from the L6–L7 junction. Within each bin, average e.p.s.p. amplitudes due to stimulation of the semimembranosus-anterior nerve branch (top) and the semimembranosus-posterior 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. Partitioning of Ia e.p.s.p.s due to stimulation of each nerve branch is evident throughout the length of the motor nucleus. This arrangement suggests a role for species specificity in the observed partitioned Ia effects.

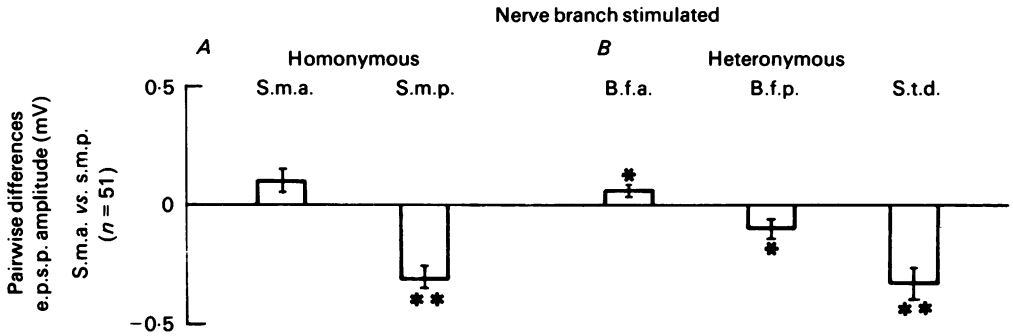

Fig. 7. Pairwise comparison of e.p.s.p. amplitudes in adjacent semimembranosus motoneurones. To minimize the effects of topographic specificity fifty-one pairs of semimembranosus-anterior and -posterior motoneurones were formed from cells in each experiment which were located within 0·5 mm of one another. Differences in e.p.s.p. amplitudes between the cells of each pair (s.m.a.–s.m.p.) in response to stimulation of a particular homonymous (*A*) or heteronymous (*B*) nerve branch were averaged for each set of pairs. The means (±S.E. of mean) of these differences are displayed here for each group of cell pairs. *A* shows the responses to stimulation of the homonymous nerve branches. The differences observed in cell pairs upon stimulation of semimembranosus-anterior are not significant; yet the e.p.s.p. amplitudes still tend to be larger in the own-branch (s.m.a.) cells ($0{\cdot}05 < P < 0{\cdot}10$; paired-sample t test). *B* illustrates significant differences in each group of cell pairs upon stimulation of the heteronymous nerve branches. * $P < 0{\cdot}025$, ** $P < 0{\cdot}0005$.

to Figs. 6 and 7*A*, species specificity in the semimembranosus motor nucleus accounted for at least some of the observed partitioning of its Ia projections.

Heteronymous connexions. Fig. 8 shows the distribution of e.p.s.p. amplitudes throughout the semimembranosus motor nucleus upon stimulation of three heteronymous nerve branches (biceps femoris-anterior, biceps femoris-posterior and semitendinosus-distal). In previous work (Botterman *et al.* 1983*a*, *b*), Ia afferents from the anterior and posterior parts of biceps femoris and semitendinosus-distal were shown to enter the cord at a more caudal level than that found in the present work for afferents from the semimembranosus muscle. If location specificity were to be a factor in establishing partitioned Ia effects in this case, larger e.p.s.p.s produced by a heteronymous nerve branch should be found for both cell groups in the caudal part of the motor nucleus. Fig. 8 shows that a contribution of location specificity was not evident in these heteronymous inputs to the semimembranosus motor nucleus.

However, the pattern of distribution of e.p.s.p. amplitudes due to stimulation of heteronymous nerve branches to the two semimembranosus cell groups did indicate some form of species specificity. Stimulation of either the biceps femoris-anterior or semitendinosus-distal nerve branch produced larger e.p.s.p.s in one cell species throughout the length of the semimembranosus motor nucleus, the effect being most pronounced with the semitendinosus-distal nerve branch. However, a similar effect was not clearly distinguishable with the biceps femoris-posterior nerve branch.

The significant differences found in Table 3 were also present in the pairwise comparisons (Fig. 7*B*), suggesting a role for species specificity in determining the distribution of e.p.s.p.s for inputs from biceps femoris-posterior and semitendinosus-

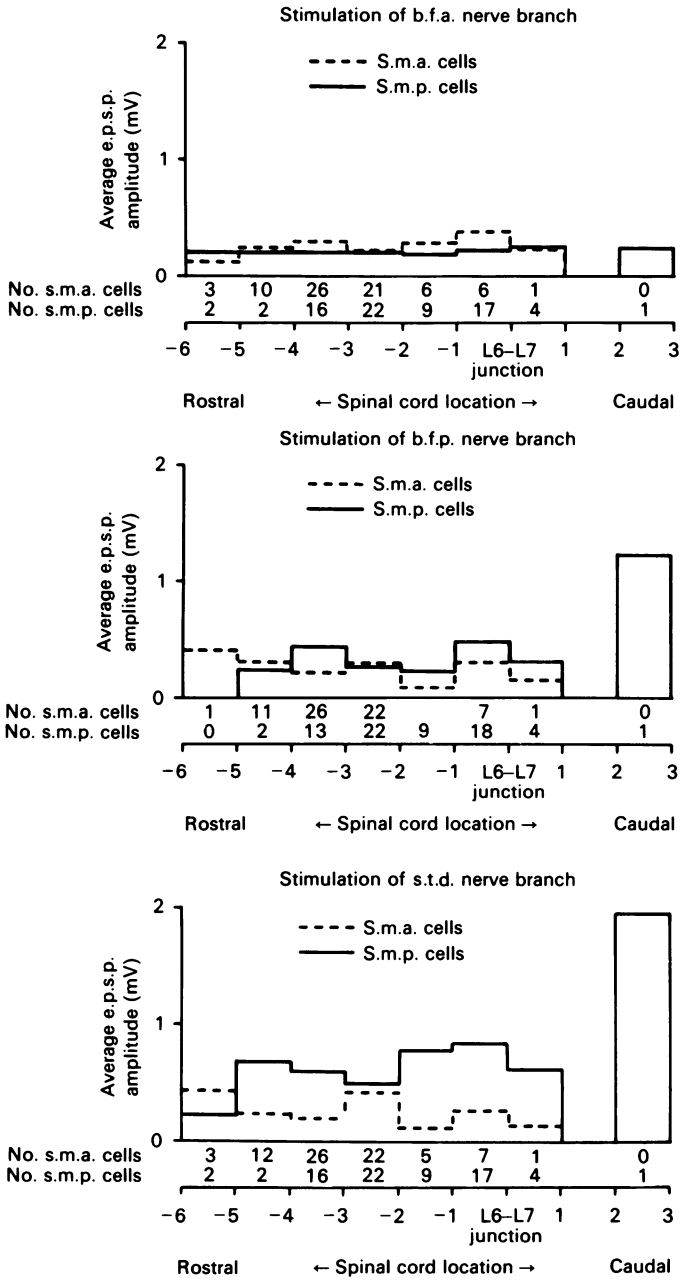

Fig. 8. Rostrocaudal distribution of heteronymous e.p.s.p. amplitudes for semimembranosus-anterior and -posterior motoneurones. As in Fig. 6 average e.p.s.p. amplitudes due to stimulation of heteronymous (i.e. biceps femoris-anterior, biceps femoris-posterior, semitendinosus-distal) nerve branches are plotted against location. Partitioned Ia effects are evident throughout the length of the semimembranosus motor nucleus upon stimulation of the nerve branches supplying biceps femoris-anterior and semitendinonsus-distal, but not biceps femoris-posterior.

distal. Given two semimembranosus cells, an anterior and a posterior one in the same relative location, stimulation of the two 'flexor' nerves, biceps femoris-posterior and semitendinosus-distal, produced larger e.p.s.p.s in the semimembranosus-posterior (hip extension–knee flexion) motoneurones than in the semimembranosus-anterior (hip extension) cells. In addition, the ability of biceps femoris-anterior ('extensor') input to 'recognize' semimembranosus-anterior over -posterior cells was significant in the pairwise comparisons (Fig. 7*B*; cf. Fig. 8), supporting the evidence in Table 3 of a difference in e.p.s.p. amplitudes due to stimulation of biceps femoris-anterior.

DISCUSSION

Partitioning of Ia e.p.s.p.s

The present results complete a sequence of studies from our laboratory that tested for the presence and extent of partitioning of monosynaptic Ia e.p.s.p.s in motor nuclei supplying cat hamstring muscles (i.e. biceps femoris: Botterman *et al.* 1983*a*; semitendinosus: Botterman *et al.* 1983*b*; and semimembranosus: present paper). As hypothesized, both biceps femoris and semimembranosus, which have regions capable of independent and different actions, show a partitioning of Ia e.p.s.p.s within their motor nuclei.

In both studies the motoneurone sample was limited largely to putative type F cells. As a result, it is not known if the type S cells would receive similar partitioned effects (cf. Lucas & Binder, 1984; Lucas *et al.* 1984; Munson *et al.* 1984). At present, this issue remains open for further investigation (for further discussion see Vanden Noven, 1984).

Results on semitendinosus (Botterman *et al.* 1983*b*), which does not show partitioning, are also consistent with the hypothesis, since this muscle would be at a functional disadvantage if its intramuscular actions were dissociated between its two in-series compartments (Bodine, Roy, Meadows, Zernicke, Sacks, Fournier & Edgerton, 1982).

Homonymous Ia e.p.s.p.s. In view of earlier statements in the influential report of Eccles & Lundberg (1958), it was necessary to test semimembranosus for a partitioning of Ia e.p.s.p.s. Although no data were presented, they reported no differences in monosynaptic Ia projections to the semimembranosus motoneurones supplying the anterior and posterior heads of the muscle.

Contrary to this earlier report, we have found evidence for a partitioning of Ia e.p.s.p.s when comparing responses of motoneurones supplying the anterior and posterior heads of semimembranosus. However, having established partitioning, the question remains as to whether it is really an 'intrahomonymous' effect or more analogous to the heteronymous connexions between soleus, medial and lateral gastrocnemius (i.e. the three heads of the triceps surae muscle).

The extent of Ia partitioning between soleus, medial and lateral gastrocnemius motor nuclei was compared by Lucas & Binder (1984) to that within the medial gastrocnemius motor nucleus. This comparison was accomplished by use of a 'weighting factor' which expressed the strength of Ia connexions from a given medial gastrocnemius nerve branch to its 'own' motoneurones relative to that of 'other' motoneurones. (The weighting factor for each nerve branch was obtained by expressing the e.p.s.p. produced by the nerve branch being considered as a fraction

of the e.p.s.p. produced by all branches. The weighting factor was then calculated as the ratio of the average fractional e.p.s.p. in the nerve branch's own motoneurones to that in its other motoneurones.) The mean value of the index for nerve branches in medial gastrocnemius was 1·8. Using the data of Eccles, Eccles & Lundberg (1957), weighting factors of 2·3, 2·7 and 3·1 were calculated for the nerves to medial gastrocnemius, lateral gastrocnemius and soleus, respectively. Thus, Ia input was shown to distinguish to a greater degree between the motoneurones innervating the three heads of triceps surae than those within the motoneurone pool innervating the single head of medial gastrocnemius.

In the case of semimembranosus, our data do not permit an examination of the strength of Ia connexions within the motor nucleus innervating only one head, but the average weighting factor between heads is 1·7. Therefore in terms of Ia projection patterns, the strength of partitioning between the two heads of semimembranosus is more similar to that seen within a single head (i.e. medial gastrocnemius) of the triceps surae muscle. Likewise our data on lateral gastrocnemius (Vanden Noven, 1984) provide a weighting factor of approximately 1·6.

Heteronymous Ia e.p.s.p.s. The results of Table 3 indicate that partitioning of heteronymous Ia projections exists within the semimembranosus motor nucleus for the hamstring inputs. The partitioned effects from biceps femoris-anterior were not as strong as those observed from biceps femoris-posterior and semitendinosus-distal. The other heteronymous inputs, gracilis and vasti, did not show localized Ia effects in the semimembranosus motor nucleus.

The lesser degree of partitioning that biceps femoris-anterior produced suggests that both semimembranosus cell groups can be activated concomitantly with the extensors while semimembranosus-posterior cells are engaged preferentially during knee flexion activity. The strong Ia partitioning effect produced by semitendinosus-distal in semimembranosus-posterior cells is consistent with the finding (Engberg & Lundberg, 1969) that the electromyographic activity produced in semimembranosus-posterior during locomotion mimics that of semitendinosus, with activity during knee flexion predominant until higher speeds are reached (e.g. trot) at which time the electromyographic activity pattern becomes more similar to that seen in hip extensors (i.e. semimembranosus-anterior, biceps femoris-anterior and adductor femoris).

Neither gracilis nor vasti Ia input showed a significant ability, based on the distribution and amplitude of monosynaptic e.p.s.p.s, to distinguish between the two groups of semimembranosus motoneurones. According to Sherrington (1910) and Eccles & Lundberg (1958), gracilis would be considered predominantly a knee flexor while the vasti would be knee extensors. Functional considerations would predict a stronger Ia connectivity pattern between gracilis and semimembranosus-posterior, whose actions are hip extension and knee flexion. The vasti (knee extensors) would not be expected to give excitatory input to semimembranosus-posterior cells due to their antagonistic knee flexor action. The absence of partitioned Ia inputs to support these functional trends within the semimembranosus motor nucleus may reflect inadequate sample sizes (forty-eight and seventy-six cells, respectively) or the lack of major synergies between these muscles (cf. however, Zajac, 1985).

Location and species specificity

The extent to which location and species specificity are present in the motor nuclei of the hamstring muscle group varies, as does the extent of partitioning of Ia e.p.s.p.s. Both may well contribute to the observed partitioning in biceps femoris (Botterman *et al.* 1983*a*). The absence of a significant topographic organization of semitendinosus motoneurones (Botterman *et al.* 1983*b*) was accompanied by a lack of partitioning of Ia e.p.s.p.s and a weak topographic pattern of Ia connexions in the motor nucleus. In the semimembranosus motor nucleus, both location and species specificity may contribute to the partitioning of Ia e.p.s.p.s. Sufficient cord-to-muscle and muscle-to-cord somatotopicity exists for location specificity to play a role in establishing the partitioned effects. That species specificity plays a role in establishing partitioning is supported in the pairwise comparisons (a test for species specificity which is not influenced by location specificity; Fig. 7). However, the magnitude of 'recognition' by the semimembranosus nerve branches of their own cells in pairwise comparisons does not account for all of the observed partitioning of Ia e.p.s.p.s (cf. Table 2 and Fig. 7).

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