J. Physiol. (1985), **364**, *pp.* 199–215
With 6 text-figures
Printed in Great Britain

INTERACTIONS BETWEEN MOTOR UNITS AND GOLGI TENDON ORGANS IN THE TIBIALIS POSTERIOR MUSCLE OF THE CAT

BY MARC D. BINDER AND CONNIE E. OSBORN*

From the Department of Physiology and Biophysics, University of Washington, School of Medicine, Seattle, WA 98195, U.S.A.

(*Received 10 October 1984*)

SUMMARY

1. The responses of Golgi tendon organs to single motor unit contractions were studied to determine whether receptors located in the same muscle region respond to a common set of motor units.

2. In each of five experiments we isolated a large fraction (25–65 %) of the motor units of the cat tibialis posterior muscle and determined to which of the units each of several tendon organs was responsive. Each tendon organ was excited by from two to fifteen of the isolated motor units, including units which produced very small forces. However, there was a much greater probability for large force units to excite a given receptor than for small force units to do so.

3. The number of motor units which produced either an 'unloading' or an 'off response' exceeded, on average, the number of motor units which excited the same tendon organ.

4. The extent to which single motor units excited both of a pair of tendon organs was examined statistically in relation to the mutual proximity of the receptors within the muscle. It was found, on average, that the closer were two receptors, the greater was the number of motor units that excited both of them.

5. These results suggest that despite the extensive territories of individual motor units, the spike trains of tendon organs may still encode information about localized muscle activity.

INTRODUCTION

The activity of individual muscle spindles and Golgi tendon organs is strongly coupled to the contraction of a specific set of a muscle's motor units (Botterman, Binder & Stuart, 1978; Binder & Stuart, 1980*b*). The strength of this mechanical coupling is primarily determined not by the force produced by the motor units, but by the anatomical relationship of the motor units with the receptor (Botterman *et al.* 1978; Binder & Stuart, 1980*a*, *b*; Cameron, Binder, Botterman, Reinking & Stuart, 1981). Receptors respond most vigorously to the contractions of motor units whose muscle fibres are located in the same region of the muscle as the receptor itself (Cameron *et al.* 1981).

* Authors' names printed in alphabetical order.

The differential sensitivity of receptors to 'regional' muscle activity suggests that receptors perform a 'sensory partitioning' (Binder, Kroin, Moore, Stauffer & Stuart, 1976) of muscle. This could provide a means for intramuscular reflex control if the information about local muscle activity were conserved in the pattern and distribution of afferent input within the homonymous motoneurone pool (Windhorst & Meyer-Lohmann, 1977; Windhorst, 1978; Botterman *et al.* 1978; Binder & Stuart, 1980*b*; Cameron *et al.* 1981). Recent experiments have demonstrated that the peripheral topographic relationships between muscle spindles and their surrounding extrafusal fibres are preserved in the pattern of synaptic connexions from Ia afferents to motoneurones (Botterman, Hamm, Reinking & Stuart, 1983; Lucas & Binder, 1984; Lucas, Cope & Binder, 1984), but the evidence for the conservation of information about regional muscle activity, in particular evidence obtained by correlation of spike trains in afferent fibres, has been inconsistent. In some cases receptors within a circumscribed muscle region have appeared to produce strongly correlated discharge patterns (Meyer-Lohmann, Riebold & Robrecht, 1974; Windhorst & Meyer-Lohmann, 1977), while in other cases the discharges of receptors located near one another appeared to be uncorrelated (Osborn & Binder, 1981). One possible explanation for the lack of correlated activity in some studies is that receptors, though located in the same general muscle region, may none the less be linked to different sets of motor units within that region and may therefore respond to different local muscle activity.

In the present study we have investigated the degree to which receptors in the same muscle region are responsive to the same set of motor units by using the interactions of Golgi tendon organs and motor units. Each tendon organ is excited by a small, discrete set of the motor units in a muscle (reviewed by Houk, Crago & Rymer, 1980), presumably those motor units of which one or two muscle fibres are attached directly to the receptor (Houk & Henneman, 1967; Stuart, Mosher, Gerlach & Reinking, 1972; Reinking, Stephens & Stuart, 1975; Binder, Kroin, Moore & Stuart, 1977; Binder, 1981; Fukami, 1981; Speilmann & Stauffer, 1983). The excitatory responses of each tendon organ are therefore related to the anatomical coupling of the receptor and the motor unit. We isolated a large fraction of the motor units in a single muscle, tibialis posterior, and identified those motor units exciting each of several tendon organs. The extent to which pairs of tendon organs were mutually excited by individual motor units was then related statistically to the relative proximity of the receptors to one another within the muscle.

A preliminary account of these results has been presented (Osborn & Binder, 1982).

METHODS

Five adult, 2·2–4·0 kg cats were deeply anaesthetized with barbiturate (Nembutal, 40 mg/kg administered intraperitoneally, with supplements given intravenously as needed during the experiment). The surgical and recording techniques used have been described previously (Binder *et al.* 1976; Binder & Stuart, 1980*a*; Binder, 1981), but details of the procedures pertinent to this report are described below.

All nerves innervating the tail and left hind limb excepting that innervating tibialis posterior were sectioned. Afferent fibres innervating Golgi tendon organs in tibialis posterior were functionally isolated by successive splitting of the cut L6 or L7 dorsal root filaments. The criteria used to identify an afferent fibre as one innervating a tendon organ were: a relatively high threshold to passive

muscle stretch, the presence of discharge during the rising phase of a maximal whole muscle twitch, and a conduction velocity greater than 60 m/s (Houk & Henneman, 1967; Matthews, 1972; Stuart *et al.* 1972; Binder, 1981).

Following isolation of a tendon organ afferent fibre, the approximate location of its receptor within the muscle was determined by probing the slackened muscle with a glass rod. Usually an afferent fibre discharged to light touch of only a small (less than 25 mm^2) area of the muscle. This area was noted on an illustration of the muscle, with particular emphasis placed on the relative locations of those receptors innervated by other tendon organ afferents whose discharge patterns were simultaneously recorded from the dorsal roots.

The ventral roots containing tibialis posterior motor axons (L6, L7 and occasionally S1) were cut and divided into fifteen to twenty filaments. Each filament was in turn divided until a single motor unit axon was functionally isolated. Both the all-or-none character of the tension produced in the muscle in response to graded stimulation of the filament and the presence of only a single-spike wave form in the stimulus-triggered average of the muscle nerve record served to verify that only a single motor axon in the filament was activated (Binder & Stuart, 1980*a*; McDonagh, Binder, Reinking & Stuart, 1980*b*). The stimulus-triggered average was also used to determine the conduction velocity of the motor axon.

Protocol

Two to four afferent fibres each innervating a different tendon organ were isolated from the dorsal root filaments, and the approximate location of each receptor in the muscle was determined. The muscle was then stretched and held at the optimum length for a twitch contraction (L_0). A single motor unit was then isolated from the ventral roots, as described above. (In a few cases when the muscle nerve record demonstrated the presence of two motor axons in a single ventral root filament, the filament was already too small to permit further division. Such filaments were retained and used to test tendon organ responses, but the presence of two motor axons was always noted with the results obtained.) The ventral root filament was stimulated at a rate of 100 pulses s^{-1} for 1·5 s, while the active force produced in the muscle (Binder, 1981) and the activity of each of the isolated tendon organ afferent fibres were recorded on separate channels of an FM tape recorder. A calibration pulse triggered by the first pulse in each stimulus train was also recorded with the tension record (Binder, 1981).

In the first three experiments, initially only two tendon organ afferents were isolated. After stimulating each ventral root filament containing a single tibialis posterior motor axon and noting the effect on the tendon organs, the filament was carefully set aside in the spinal bath. When no more motor axons could be found, one or two other tendon organ afferent fibres were isolated from the dorsal roots, and their responses to the contractions of the set of motor axons previously isolated were recorded. In most cases motor axons could be re-identified for repeated testing based upon the location of the ventral root filament in the spinal bath, the record of the tetanic tension produced by each unit, and the profiles of the axonal spike wave forms obtained from the computer-averaged muscle nerve record.

In the last two experiments, four tendon organ afferent fibres were isolated at the outset. After each motor axon was isolated and tested, the filament containing its axon was then removed. At the end of these experiments, the muscle nerve was dissected until the two main branches entering the hilus of the muscle could be separated (Chin, Cope & Pang, 1962). By cutting one nerve branch while recording the activity of all four afferent fibres, the nerve branch in which each fibre travelled was determined.

Analysis

The simultaneously recorded motor unit tension profiles and tendon organ afferent discharges were reproduced on a two-channel chart recorder for off-line analysis. The average firing rate of each afferent fibre was measured during the last second of the 1·5 s tetanus. If the afferent fibre discharged in the absence of motor unit contraction, this spontaneous rate was measured for 1 s prior to motor unit contraction and was subtracted from the rate observed during the tetanus to obtain the average contraction-evoked discharge rate. Tetanic tension was measured for each motor unit at 1 s after the beginning of the stimulus train.

Tendon organ responses to motor unit contractions were classified using the terminology of Stuart *et al.* (1972). An increase in tendon organ firing rate during motor unit contraction was classified

as an 'in-series' or 'loading' response. A decrease in spontaneous rate during contraction was considered an 'in-parallel' or 'unloading' response, and an 'off' response was one in which a previously silent tendon organ discharged only during the falling phase of the contraction.

RESULTS

Motor unit sampling in the tibialis posterior muscle

Tibialis posterior is a small hind-limb muscle innervated by approximately sixty motoneurones (Boyd & Davy, 1968) which are distributed over two spinal segments. This broad distribution facilitates the isolation of a large percentage of the motor units in an individual experiment (McDonagh *et al.* 1980*b*). In the five experiments described below, a total of 141 ventral root filaments each containing a single functional motor unit, and sixteen filaments each containing two motor units were isolated. In each experiment 25–65 % of the muscle's motor units were functionally isolated.

Conduction velocity was measured for 109 single motor units in four of the five experiments. The mean, $79{\cdot}8 \pm 5{\cdot}0$ (S.D.) m s^{-1}, is within the range previously reported for motor axons in tibialis posterior ($70 \pm 8{\cdot}4$, $81 \pm 8{\cdot}1$: Boyd & Davy, 1968; $87{\cdot}4 \pm 14{\cdot}2$: McDonagh *et al.* 1980*b*). A more sensitive measure of possible sample bias is the distribution of tetanic tension for single motor units. The range of tensions for motor units in our study, 1·5–220 g, is nearly identical with that previously reported (McDonagh *et al.* 1980*b*), but the distributions of tension are significantly different (Fig. 1). In the present study the proportion of motor units producing 50–100 g of tetanic tension is higher than that in the McDonagh *et al.* (1980*b*) study, whereas the proportion of motor units producing less than 25 g is lower ($P < 0{\cdot}05$; χ^2 test, Mosteller & Rourke, 1973).

Types of tendon organ responses to motor unit contraction

A total of nineteen tendon organs were studied. The receptor sites, estimated by probing the muscle as described in the Methods, were found throughout the longitudinal extent of the muscle in both the anterior ($n = 9$) and posterior ($n = 10$) compartments (Chin *et al.* 1962). The tendon organs exhibited the same types of responses to tetanic contractions of single motor units (Table 1) as those described for tendon organs in several other cat hind-limb muscles (Houk & Henneman, 1967; Stuart *et al.* 1972; Stauffer & Stephens, 1975; Reinking *et al.* 1975; Jami & Petit, 1976*a*, *b*; Gregory & Proske, 1979).

Tendon organs were either loaded or unloaded during motor unit contraction, or showed an off response, a short burst on the falling phase of tension in an otherwise silent receptor (Stuart *et al.* 1972). In our study two to fifteen (mean, eight) of the motor units tested produced loading responses in a tendon organ. These range and mean values are comparable to those observed for tendon organs in other hind-limb muscles (reviewed by Binder & Stuart, 1980*b*; Houk *et al.* 1980). However, the number of motor units which produced either an unloading or off response (mean, eleven; range one to twenty-two) exceeded, on average, the number of motor units which excited the same tendon organ. Particularly striking examples of this were the three receptors with spontaneous activity which were excited by an average of nine motor

units, but were unloaded by every other motor unit tested ($n = 17$, $n = 18$, $n = 22$). No comparable data on the frequency of unloading or off responses are available for tendon organs of other hind-limb muscles.

Table 1 lists the fractions of sampled motor units which produced each type of response in the nineteen tendon organs studied. Note that not all tendon organs in an experiment were tested with the same number of motor units. As discussed above in the Methods, in three experiments initially only one pair of tendon organ afferents was isolated and tested with all of the isolated motor units and then a second pair

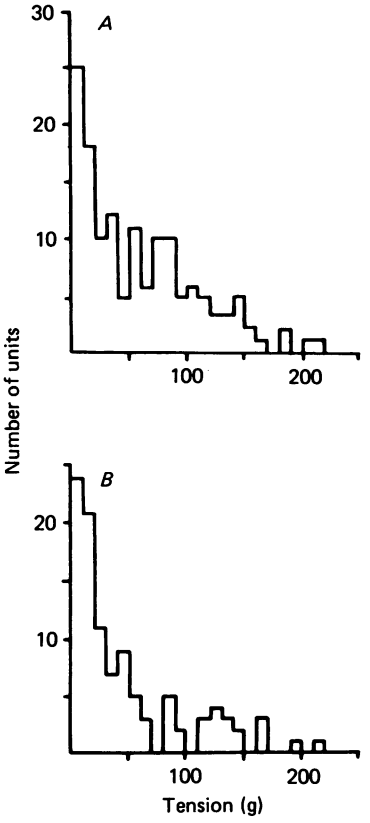


Fig. 1. Distribution of maximal tetanic forces of motor units in tibialis posterior. *A*, data derived from the present study of 141 motor units. *B*, data taken from the study of McDonagh *et al.* (1980*b*) for 104 motor units.

of afferent fibres was identified and tested. During the second series of tests motor units were sometimes lost; consequently, there were fewer motor units available for testing the responses of the second pair of tendon organs. Furthermore, some Golgi tendon organs such as no. 3 in experiment no. 5, showed both unloading and off responses. The unloading responses occurred when the tendon organ was spontaneously active prior to the motor unit contraction, while the off response occurred when the tendon organ was silent prior to the motor unit contraction. Such alternation between epochs of silence and spontaneous activity was probably due to slight changes in the passive tension of the muscle.

TABLE 1. Summary of responses of Golgi tendon organs in tibialis posterior to contractions of single motor units. Listed on the left side of the table are the numbers of motor units tested for each tendon organ (G.t.o.) and the numbers of motor units which loaded each. On the right side are listed the fractions of the motor units tested which elicited either a loading, an unloading, an off or no response from each tendon organ. Asterisks denote experiments in which tendon organ responses to ventral root filaments containing two motor axons from tibialis posterior were included in the total (fifteen filaments with two motor axons in experiment no. 2; one filament with two motor axons in experiment no. 3)

				% of motor units which produced:			
Expt. no.	G.t.o. no.	No. motor units tested	No. loading motor units	Loading response	Off response	Unloading response	No response
1	1	32	10	31	13	28	28
	2	32	11	34	0	34	31
	3	26	8	31	38	0	31
	4	26	5	19	0	8	73
2*	1	54	10	19	15	0	66
	2	54	15	28	11	0	61
	3	39	10	26	19	0	55
	4	39	10	26	37	0	37
3*	1	27	5	19	48	0	33
	2	27	8	30	30	0	40
	3	24	6	25	0	75	0
4	1	15	6	40	27	0	33
	2	15	2	13	67	0	20
	3	15	3	20	40	0	40
	4	15	6	40	33	0	27
5	1	30	13	43	0	57	0
	2	30	8	27	0	73	0
	3	30	5	17	60	17	7
	4	30	8	27	70	3	0

Characteristics of loading motor units in tibialis posterior

Previous analyses of motor units which produce loading responses from tendon organs have shown that the conduction velocity and tetanic tension ranges for loading motor units are similar to those for the whole motor unit population (Reinking *et al.* 1975; Jami & Petit, 1976*a*, *b*; Gregory & Proske, 1979). This finding has led to the hypothesis that tendon organs are loaded by a random sample of the motor unit population (Reinking *et al.* 1975; Houk *et al.* 1980). The large samples of motor units we obtained in these experiments permitted us to test this hypothesis by comparing the distributions of tetanic tension for loading and non-loading motor units.

In Fig. 2 the distributions of tetanic forces produced by the motor units in our sample are shown, with the distributions of loading and non-loading motor unit forces indicated by continuous and dotted lines, respectively. As has been noted before, the loading motor units were markedly heterogeneous in the forces produced and included units producing the smallest forces as well as ones producing the largest (Reinking *et al.* 1975; Jami & Petit 1976*a*, *b*; Gregory & Proske, 1979). However, the two distributions are significantly different. There were more large force units (> 80 g) in the set of loading motor units than would be expected from a random selection of motor units from our sample ($P < 0{\cdot}05$; χ^2 test).

Tendon organ firing rate and motor unit force

The relationship between tendon organ firing rate during motor unit tetanus and the tension produced by the motor unit is shown in Fig. 3. Even in this large sample ($n = 138$) the correlation between the two variables is weak ($r = 0{\cdot}25$; $P < 0{\cdot}005$), confirming for tibialis posterior the observation made about tendon organs and motor units in studies of other cat muscles (Stauffer & Stephens, 1975; Reinking *et al.* 1975; Jami & Petit, 1976*a*, *b*; Gregory & Proske, 1979; Houk *et al.* 1980; Binder, 1981; Fukami, 1981; Cameron *et al.* 1981). The correlation is still weak when only the spontaneously active receptors are included in the sample ($n = 56$; $r = 0{\cdot}32$; $P < 0{\cdot}02$).

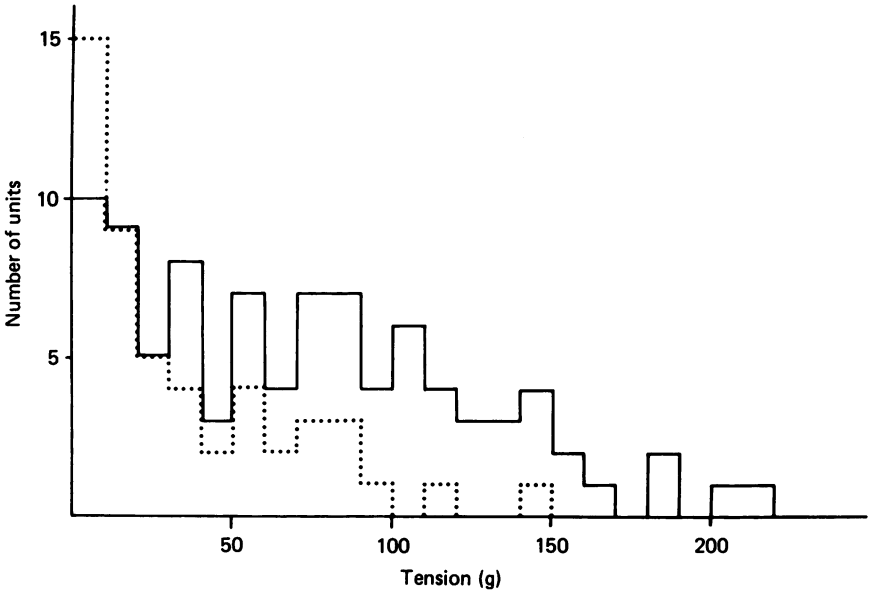


Fig. 2. Distributions of the maximal tetanic tensions produced by motor units which did (continuous line) or did not (dotted line) excite at least one of the tendon organs studied. Of the 141 motor units tested, 91 excited at least one of the isolated tendon organs. The two distributions are significantly different ($P < 0{\cdot}05$; χ^2 test).

Tendon organ proximity and motor unit sharing

A principal aim of this study was to determine the extent to which pairs of tendon organs are mutually excited by individual motor units with respect to the relative proximity of the receptors to one another within the muscle. As described in the Methods, we determined the approximate location of each of the tendon organs we studied, with particular attention to their positions relative to the longitudinal tendon that bisects tibialis posterior (Chin *et al.* 1962). From the five experiments, we obtained data from a total of twenty-seven pairs of tendon organs.

Fig. 4 summarizes the anatomical and physiological results from a single experiment. On the left is a schematic diagram of tibialis posterior which features the longitudinal tendon that defines the anterior and posterior compartments of the

muscle, the bifurcated muscle nerve and the approximate locations of the four tendon organs that were studied. The tabulations on the right list the number of motor units that were tested with each tendon organ, the number that produced loading responses in each, and the number of motor units that produced loading responses in both members of each of the six tendon organ pair combinations. These data illustrate the strong relationship between the relative proximity of tendon organs within the muscle and their tendency to 'share' motor units. The two closest receptors, labelled 2 and

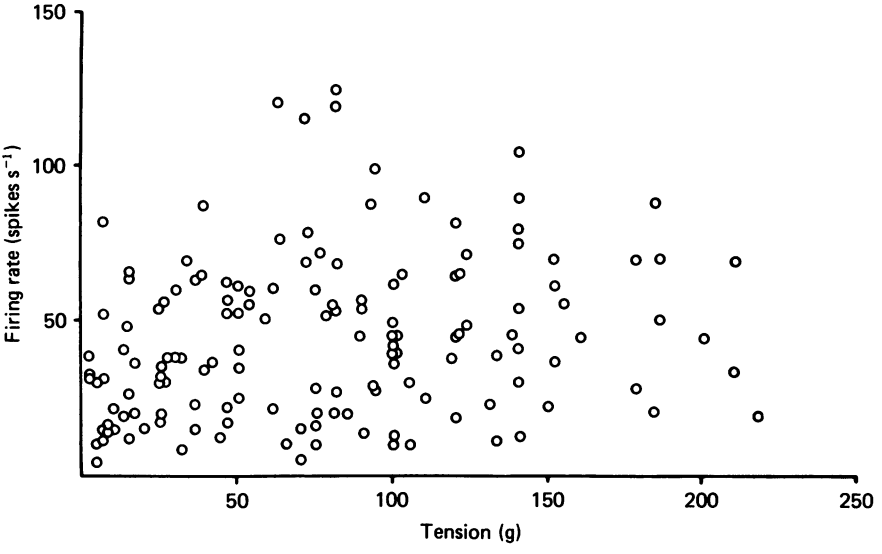
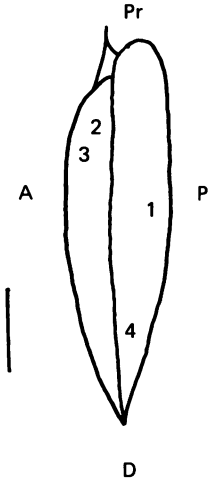


Fig. 3. Lack of relationship between the firing rates of tendon organs and the tetanic tensions produced by motor units exciting them. Firing rate was defined as the difference between the spontaneous rate, if any, of a tendon organ and the average firing rate during the last second of the 1·5 s tetanus.

3, both responded to gentle probing of the same muscle region, and six of the eight motor units that loaded receptor 3 also loaded receptor 2. In contrast, the tendon organ pairs showing the greatest spatial separation within the muscle (receptors 2 and 4; and receptors 3 and 4) had no motor units in common.

To examine this relationship more systematically, the entire sample of tendon organ pairs ($n = 27$) was divided into three groups. The first group ($n = 4$), called close receptors, consisted of those pairs in which both receptors responded to mechanical probing of the same muscle region. The second group ($n = 10$), called distant receptors, consisted of pairs with one receptor in the proximal quarter of the muscle and the other in the distal quarter. The remaining thirteen pairs of tendon organs comprised the third group, for which the distance separating the receptors was intermediate to the distances defining the first and second groups. The distributions of motor unit sharing for all the tendon organ pairs are presented in Fig. 5. The values for the close and distant groups of tendon organ pairs are shown by the cross-hatched and blackened areas, respectively, overlying the values observed for the entire sample. The mean number of motor units shared by pairs of tendon organs in each group differed significantly from the mean number of shared units in each of the other

two groups (Student's t test; $P < 0{\cdot}01$). The close pairs shared an average of $4{\cdot}5 \pm 1{\cdot}7$ motor units and included all pairs sharing more than four units. In contrast, the distant pairs shared an average of only $0{\cdot}7 \pm 0{\cdot}95$ motor units and half of the distant pairs had no motor units in common. The intermediate pairs shared an average of $2{\cdot}1 \pm 1{\cdot}2$ motor units, significantly more than the distant pairs, but significantly fewer than the close pairs.



Tendon organ	Motor units loading each tendon organ	Motor units tested
1	10	32
2	11	32
3	8	26
4	5	26

Tendon organ pair	Motor units loading both
1, 2	2
1, 3	1
1, 4	2
2, 3	6
2, 4	0
3, 4	0

Fig. 4. Summary of tendon organ excitation by motor units in one experiment. To the left is a schematic of tibialis posterior, showing the intramuscular tendon which delineates the anterior and posterior compartments (Chin *et al.* 1962). Each number on the drawing represents the estimated location of a tendon organ whose afferent fibre was isolated in this experiment. Tendon organs 2 and 3 were located in the anterior compartment of the muscle, and tendon organs 1 and 4 were in the posterior compartment. In addition, the receptor areas of tendon organs 2 and 3 were overlapping (see text). The number of motor units tested for each of the four tendon organs and the number of motor units loading each are listed on the right. Also listed are the numbers of motor units which loaded both members of a pair of tendon organs. Vertical bar represents 1 cm. Pr = proximal; A = anterior; P = posterior; D = distal.

We thought it possible that a second form of spatial relationship between tendon organs and motor units might be imposed by the longitudinal tendon in tibialis posterior, which delineates the anterior and posterior compartments of the muscle (Chin *et al.* 1962). Thus, the extent of motor unit sharing for pairs of tendon organs with both receptors in the same muscle compartment ($n = 10$) was compared with that for pairs of tendon organs with one receptor located in each compartment ($n = 17$). As shown in Fig. 6, the distributions of motor unit sharing appear quite distinct for these two groups of tendon organ pairs. However, the mean number of

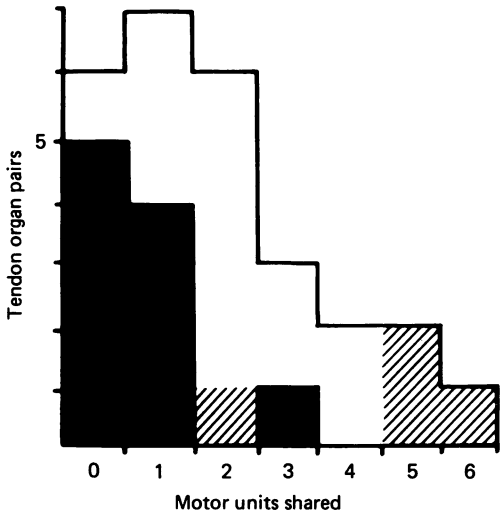


Fig. 5. Histogram showing the number of loading motor units shared by different pairs of tendon organs. The data derived from 'close' receptors (see text) are cross-hatched, and those from 'distant' receptors are blackened. The average number of motor units shared by 'close' ($4{\cdot}5 \pm 1{\cdot}7$), 'intermediate' ($2{\cdot}1 \pm 1{\cdot}2$) and 'distant' ($0{\cdot}7 \pm 0{\cdot}95$) pairs of tendon organs all differed significantly ($P < 0{\cdot}01$; Student's t test).

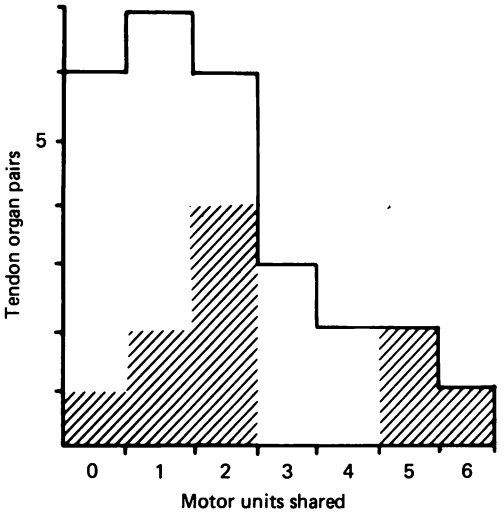


Fig. 6. Comparison of motor unit sharing for pairs of tendon organs with both receptors in the same compartment (cross-hatched) *versus* pairs with receptors located in different compartments.

shared motor units for tendon organ pairs with receptors located in the same muscle compartment ($2{\cdot}6 \pm 2{\cdot}0$) was not significantly different from that for tendon organ pairs with receptors located in different compartments ($1{\cdot}5 \pm 1{\cdot}4$). It is possible that a larger sample size would yield significant differences between these two groups, but it seems clear that the extent of motor unit sharing is strongly related to the distance

separating two tendon organs in tibialis posterior, regardless of which compartment they are located in.

DISCUSSION

We have found that tendon organs located in the same region of tibialis posterior are much more likely to be excited by the same motor units than are tendon organs in widely separated regions of the muscle. If tendon organs make connexions with a random selection of local muscle fibres (Tello, 1917; Zelena & Soukup, 1977), then the results of this study are best explained by regional differences in the concentration of muscle fibres for individual motor units. The probability of any of a motor unit's fibres attaching to tendon organs in a given muscle region should be determined primarily by the relative density of the motor unit's fibres within that region. Pairs of tendon organs in the same muscle region, embedded in a similar milieu of unequally represented motor units, would thus be more likely to attach to muscle fibres of the same motor units than would pairs of tendon organs located in different regions.

In contrast to the situation in medial and lateral gastrocnemius, in which the muscle fibres of each motor unit are confined almost entirely to a single compartment (Letbetter, 1974; Farina & Letbetter, 1977; Botterman *et al.* 1978; English & Weeks, 1982), in tibialis posterior rigid compartmentalization of the constituent fibres of a motor unit does not seem to occur. Instead, the distribution of muscle fibres of a motor unit is better described as a gradient of muscle fibre density, with muscle fibres of a unit distributed on each side of the longitudinal tendon, but found in varying concentrations along the proximal–distal axis of the muscle. The bilateral distribution of motor unit fibres with respect to the intramuscular tendon is demonstrated by the present finding of motor unit sharing by tendon organ pairs even when the two receptors are located on opposite sides of the tendon. Moreover, the proximo-distal extent of motor unit territories in tibialis posterior is underscored by the fact that two receptors, one located at the proximal and one located at the distal extreme of the muscle, may share excitation from a single motor unit.

The description of motor unit territories suggested by the present data is supported by observations on tibialis posterior motor units (J. C. McDonagh, M. D. Binder, R. M. Reinking & D. G. Stuart, unpublished). The territories of single motor units were mapped by glycogen depletion techniques and were found to extend throughout the muscle from the proximal to the distal ends, and on either side of the intramuscular tendon. As is consistent with the inferences of the present study, muscle fibres of a single motor unit were also found to be unequally represented in different proximo-distal regions of this muscle.

It is interesting that in tibialis posterior there is no strong relationship between the nerve branch in which the motor axon travels and the region of the muscle occupied by its constituent muscle fibres. In other muscles, the bifurcation of the nerve is often a hallmark of restrictions on the extent of the muscle occupied by each motor unit (Eccles & Sherrington, 1930). In medial gastrocnemius, for example, the territories of motor units with axons in the same branch are all localized within the same muscle region, i.e. an intramuscular compartment (Letbetter, 1974). In addition, the receptors within a compartment are innervated by afferent fibres

travelling in the nerve branch containing the motor axons which innervate the compartment (Farina & Letbetter, 1977). The division of the muscle nerve into several branches therefore presages a compartmentalization of afferent and efferent terminations within the muscle. In tibialis posterior, nerve branching is associated neither with localization of motor units (J. C. McDonagh, M. D. Binder, R. M. Reinking & D. G. Stuart, unpublished), nor with reciprocal compartmentalization of muscle fibres and muscle receptors. The organization of efferent fibres in tibialis posterior suggests that individual motor axons might bifurcate at the same juncture as the main nerve, as observed previously by Eccles & Sherrington (1930).

The findings of the present experiments suggest that restriction of the constituent fibres of a motor unit to a discrete muscle compartment is not a requirement for the preferential sensitivity of a muscle receptor to activity in a particular region of the muscle. Unless the muscle is completely homogeneous in its intermixture of muscle fibres for all motor units, there will exist regional differences in concentration of the muscle fibres of each motor unit. Due to these regional differences and the ensuing unequal probabilities of attachments between receptors and fibres from different motor units, receptor activity may in fact include information as to the regions of muscle activated by individual motor unit activity (Binder *et al.* 1977; Botterman *et al.* 1978; Binder & Stuart, 1980*b*).

Motor units loading tendon organs

The large sample size required for our analysis of the spatial organization of motor units and tendon organs allowed examination of the characteristics of motor units which loaded or unloaded tendon organs. Tendon organs in tibialis posterior behave like those in other hind-limb muscles and conform to the model of tendon organ behaviour proposed by Houk & Henneman (1967). The tendon organs we studied were excited by from two to fifteen single motor units, with a mean number of eight motor units. Similar values have been obtained for tendon organs in soleus, peroneus brevis, plantaris, medial gastrocnemius, and tibialis anterior (Houk & Henneman, 1967; Reinking *et al.* 1975; Jami & Petit, 1976*a*, *b*; Gregory & Proske, 1979; Binder, 1981).

The mean number of eight loading motor units per tendon organ we observed in tibialis posterior may be an underestimate of the actual number of loading motor units, since not all of the muscle's motor units could be isolated in each experiment. However, we rarely noted that an excitatory response to stimulation of a ventral root filament in one or more of the tendon organs we were studying was 'lost' following subdivision of that filament. None the less, inspection of Table 1 indicates that we generally found more loading motor units per tendon organ in those experiments in which we isolated a greater number of motor units. Thus, the actual mean number of loading motor units might be closer to eleven, a value consistent with the anatomical data from tendon organs in several cat hind-limb muscles (Bridgeman, 1970; Barker, 1974).

Motor units that excite tendon organs in tibialis posterior are a heterogeneous sample of the muscle's population and include units producing very small forces as well as ones producing very large forces. However, although small force units occurred in the sets of loading motor units, for each receptor there was a much greater probability that large force rather than small force units would excite the tendon

organ. There have been no comparable experiments to test this finding in other muscles, probably because the experiment requires the survey of a significant fraction of the motor units in a muscle. Technical difficulties make such a survey impractical for most muscles.

The finding that more large force than small force motor units excite a given receptor is probably not due to a special ability of large force units to excite a tendon organ without a fibre attached to it (an 'off-line' motor unit: Houk & Henneman, 1967). As predicted by Binder *et al.* (1977), studies on tendon organs *in vitro* have demonstrated that the contraction of any of the muscle fibres attached in series to the receptor is sufficient to excite the tendon organ (Fukami & Wilkinson, 1977; Fukami, 1981). Moreover, the number of motor units which, on average, excite tendon organs does not exceed the average number of muscle fibres attached to a tendon organ, suggesting that off-line motor units do not excite them (Houk *et al.* 1980; see however Stuart, Goslow, Mosher & Reinking, 1970). Additional evidence against excitation by off-line units comes from experiments on tendon organs in soleus. Ventral root filaments which, when stimulated individually, did not excite a tendon organ, remained ineffective when stimulated concurrently, even though their combined force was 100 times greater than the force of one of the loading motor units (Binder, 1981).

If muscle fibres are attached at random to tendon organs, and if only motor units with fibres attached to a tendon organ excite it, then our data suggest that these receptors are located in areas with relatively large numbers of fibres from large force units. This could be a consequence of the presence of a greater number of muscle fibres in large force than in small force motor units, or it could reflect differences in the distribution of fibres from different motor unit types in tibialis posterior. Analysis of the motor unit and muscle fibre composition of tibialis posterior (McDonagh, Binder, Reinking & Stuart, 1980*a*, *b*) suggests that it is the greater number of muscle fibres in the large force units that accounts at least in part for the present findings.

The arrangements of tendon organs in tibialis posterior differs from that suggested for tendon organs in highly compartmentalized muscles (Botterman *et al.* 1978). In those muscles, tendon organs are thought to be located in regions rich in the slow oxidative muscle fibres which comprise the low force motor units. The close proximity of the muscle receptors and the constituents of small force motor units has been suggested to subserve a preferential sensitivity of the receptors to the activity of low force units; a sensitivity which in turn indicates a relatively greater role for these receptors during the low force contractions in which these motor units predominate than in more forceful contractions (Botterman *et al.* 1978; Binder & Stuart, 1980*b*). Our data suggest, however, that in tibialis posterior, tendon organs are embedded in regions rich in large force rather than small force muscle fibres, and thus, tendon organs in this muscle may have no special role in monitoring low force, finely graded contractions (Botterman *et al.* 1978; Binder & Stuart, 1980*b*).

Motor units producing unloading and off responses

Although the different types of tendon organ response to motor unit contractions have been described before (Houk & Henneman, 1967; Stuart *et al.* 1972; Reinking *et al.* 1975; Jami & Petit, 1976*a*, *b*; Binder *et al.* 1977; Gregory & Proske, 1979;

Fukami, 1981), there have been no previous reports of the fractions of motor units in a muscle capable of eliciting those responses from a tendon organ. In this study, a mean of $70{\cdot}3 \pm 21{\cdot}9\%$ of the motor units studied in association with each of the nineteen tendon organs produced a response of some kind, either a loading, unloading, or off response. Moreover, for the three tendon organs which maintained spontaneous activity throughout the course of an experiment, the contraction of every motor unit tested either increased or decreased the firing rate of the receptor. This suggests that once a tendon organ is activated in this muscle either by motor unit contraction and/or passive tension, its response is not solely the result of activity in the small number of motor units which directly excite the receptor. Rather, its discharge pattern is further influenced by every motor unit actively contracting in the muscle. Since most tendon organs were excited by at least one motor unit with small contractile force, most tendon organs will be excited at low levels of force production, and the firing rate will be modulated thereafter by the contraction of each successively recruited motor unit (Houk *et al.* 1980; Crago, Houk & Rymer, 1982).

Functional significance of unloading and off responses

The sensitivity of activated tendon organs to unloading may be reflected in the behaviour of these receptors to both single motor unit contractions and whole muscle contractions. The firing rate of tendon organs in tibialis posterior as in other hind-limb muscles (Houk & Henneman, 1967; Stauffer & Stephens, 1975; Reinking *et al.* 1975; Jami & Petit, 1976*b*; Gregory & Proske, 1979), is generally uncorrelated with the force of a single motor unit which excites the receptor. It has been suggested that the failure of large force motor units to produce the greatest response in tendon organs is due to the unloading effect of the muscle fibres in the unit which are arranged not in series, but in parallel, with the receptor (Fukami, 1981). Since large force motor units generally have more muscle fibres, which individually have higher specific tensions than do fibres from small force units (McDonagh *et al.* 1980*a*; Burke, 1981), the off-line fibres of large force motor units could be more effective than those of small force units in unloading receptors. The present findings about motor unit unloading of tendon organs lend support to this hypothesis. If a spontaneously active tendon organ can be unloaded by every motor unit which does not directly excite it, then it is possible that the activity of one or two fibres attached to a tendon organ could be reduced significantly by the contraction of off-line units, which would alter receptor response to whole muscle contraction (Binder, 1981). Therefore, it should not be surprising that the response of a tendon organ to contraction of combinations of its loading motor units fails to predict tendon organ response to whole muscle force. In the latter case, increments in force elicit both strong excitation and strong unloading as both in-series and in-parallel motor units exert their influence on each receptor. The result is a linear relationship of firing rate with whole muscle force (Crago *et al.* 1982) quite unlike the relationship observed to single motor units (Houk & Henneman, 1967; Reinking *et al.* 1975; Stauffer & Stephen, 1975; Jami & Petit, 1976*a*, *b*; Gregory & Proske, 1979), or to several in-series motor units (Gregory & Proske, 1979).

Finally, any tendency for tendon organs to be unloaded by off-line motor units will reflect back on the topographic scheme described above for interactions between tendon organs and motor units. By identifying the motor units which excited several

tendon organs, we found a tendency for adjacent receptors to be excited by the same motor unit. However, the unloading of receptors by off-line motor units, as suggested by our results, may well alter the effects of regional muscle activity on tendon organ response. Our results suggest that the combined effects of loading and unloading motor units will determine the behaviour of tendon organs during muscle contraction, and therefore the persistence of any sensory partitioning (Binder *et al.* 1976; Botterman *et al.* 1978; Binder & Stuart, 1980*a*, *b*) during whole muscle activity.

We thank Dr R. C. Kramis for his assistance throughout all phases of this study and Drs T. M. Hamm, R. E. Poppele and D. G. Stuart for reviewing the manuscript. This work was supported by National Institute of Health Grant NS 15404, Teacher–Investigator Development Award NS 00345, and National Science Foundation Grant BNS-06223.

REFERENCES

BARKER, D. (1974). Morphology of muscle receptors. In *Handbook of Sensory Physiology*, vol. III/2, ed. HUNT, C. C., pp. 1–190. New York: Springer.

BINDER, M. D. (1981). Further evidence that the Golgi tendon organ monitors the activity of a discrete set of motor units within a muscle. *Experimental Brain Research* **43**, 186–192.

BINDER, M. D., KROIN, J. S., MOORE, G. P., STAUFFER, E. K. & STUART, D. G. (1976). Correlation analysis of muscle spindle responses to single motor unit contractions. *Journal of Physiology* **257**, 325–336.

BINDER, M. D., KROIN, J. S., MOORE, G. P. & STUART, D. G. (1977). The response of Golgi tendon organs to single motor unit contractions. *Journal of Physiology* **271**, 337–349.

BINDER, M. D. & STUART, D. G. (1980*a*). Responses of Ia and spindle Group II afferents to single muscle unit contractions. *Journal of Neurophysiology* **43**, 621–629.

BINDER, M. D. & STUART, D. G. (1980*b*). Motor unit–muscle receptor interactions: design features of the neuromuscular control system. In *Progress in Clinical Neurophysiology. Spinal and Supraspinal Mechanisms of Voluntary Motor Control and Locomotion*, vol. 8, ed. DESMEDT, J., pp. 72–98. Basel: Karger.

BOTTERMAN, B. R., BINDER, M. D. & STUART, D. G. (1978). Functional anatomy of the association between motor units and muscle receptors. *American Zoologist* **18**, 135–152.

BOTTERMAN, B. R., HAMM, T. M., REINKING, R. M. & STUART, D. G. (1983). Localization of monosynaptic Ia excitatory post-synaptic potentials in the motor nucleus of the cat biceps femoris muscle. *Journal of Physiology* **338**, 355–377.

BOYD, I. A. & DAVEY, M. R. (1968). *Composition of Peripheral Nerves*. Edinburgh: E. & S. Livingstone, Ltd.

BRIDGEMAN, C. F. (1970). Comparisons in structure of tendon organs in the rat, cat and man. *Journal of Comparative Neurology* **138**, 369–372.

BURKE, R. E. (1981). Motor units: anatomy, physiology and functional organization. In *American Physiological Society Handbook of Physiology Series*, vol. 4, *Motor Systems*, ed. BROOKS, V. B. Bethesda: American Physiological Society.

CAMERON, W. E., BINDER, M. D., BOTTERMAN, B. R., REINKING, R. M. & STUART, D. G. (1981). 'Sensory partitioning' of the cat medial gastrocnemius muscle by its muscle spindles and tendon organs. *Journal of Neurophysiology* **46**, 32–47.

CHIN, N. K., COPE, M. & PANG, M. (1962). Number and distribution of spindle capsules in seven hind limb muscles of the cat. In *Symposium on Muscle Receptors*, ed. BARKER, D. Hong Kong: Hong Kong University Press.

CRAGO, P. E., HOUK, J. C. & RYMER, W. Z. (1982). Sampling of total muscle force by tendon organs. *Journal of Neurophysiology* **47**, 1069–1083.

ECCLES, J. C. & SHERRINGTON, C. (1930). Numbers and contraction-values of individual motor units examined in some muscles of the limb. *Proceedings of the Royal Society* B **106**, 326–357.

ENGLISH, A. W. & WEEKS, O. I. (1982). Compartmentalization of muscle units in cat lateral gastrocnemius muscle. *Neuroscience Abstracts* **8**, 959.

FARINA, J. A. & LETBETTER, W. D. (1977). Organization of primary spindle afferents with response to intramuscular branches of medial gastrocnemius nerve. *Journal of the South Carolina Medical Association* **73**, 15–16.

FUKAMI, Y. (1981). Responses of isolated Golgi tendon organs of the cat to muscle contraction and electrical stimulation. *Journal of Physiology* **318**, 429–443.

FUKAMI, Y. & WILKINSON, R. S. (1977). Responses of isolated Golgi tendon organs of the cat. *Journal of Physiology* **265**, 673–689.

GREGORY, J. E. & PROSKE, U. (1979). The response of Golgi tendon organs to stimulation of different combinations of motor units. *Journal of Physiology* **295**, 251–262.

HOUK, J. C., CRAGO, P. E. & RYMER, W. Z. (1980). Functional properties of Golgi tendon organs. *Progress in Clinical Neurophysiology*, vol. 8, *Segmental Motor Control in Man*, ed. DESMEDT, J. E., pp. 33–43. Basel: Karger.

HOUK, J. & HENNEMAN, E. (1967). Responses of Golgi tendon organs to active contractions of the soleus muscle of the cat. *Journal of Neurophysiology* **30**, 466–481.

JAMI, L. & PETIT, J. (1976*a*). Heterogeneity of motor units activating single Golgi tendon organs in cat leg muscles. *Experimental Brain Research* **24**, 485–493.

JAMI, L. & PETIT, J. (1976*b*). Frequency of tendon organ discharges elicited by the contraction of motor units in cat leg muscles. *Journal of Physiology* **261**, 633–645.

LETBETTER, W. D. (1974). Influence of intramuscular nerve branching on motor unit organization in medial gastrocnemius muscle. *Anatomical Record* **178**, 402.

LUCAS, S. M. & BINDER, M. D. (1984). Topographic factors in the distribution of homonymous group Ia afferent input to cat medial gastrocnemius motoneurons. *Journal of Neurophysiology* **51**, 50–63.

LUCAS, S. M., COPE, T. C. & BINDER, M. D. (1984). Analysis of individual homonymous Ia afferent epsps in an homonymous motoneuron pool with respect to muscle topography. *Journal of Neurophysiology* **51**, 64–74.

MATTHEWS, P. B. C. (1972). *Mammalian Muscle Receptors and Their Central Actions*. London: Arnold.

MCDONAGH, J. C., BINDER, M. D., REINKING, R. M. & STUART, D. G. (1980*a*). A commentary on muscle unit properties in cat hindlimb muscle. *Journal of Morphology* **166**, 217–230.

MCDONAGH, J. C., BINDER, M. D., REINKING, R. M. & STUART, D. G. (1980*b*). Tetrapartite classification of motor units of cat tibialis posterior. *Journal of Neurophysiology* **44**, 696–712.

MEYER-LOHMANN, J., RIEBOLD, W. & ROBRECHT, D. (1974). Mechanical influence of the extrafusal muscle on the static behavior of deefferented primary muscle spindle ending in cat. *Pflügers Archiv* **352**, 267–278.

MOSTELLER, F. & ROURKE, R. E. K. (1973). *Sturdy statistics: Nonparametric and Order Statistics*. Reading, MA: Addison-Wesley.

OSBORN, C. E. & BINDER, M. D. (1981). Correlation analysis of muscle spindle and tendon organ afferents in active muscle. *Neuroscience Abstracts* **7**, 409.

OSBORN, C. E. & BINDER, M. D. (1982). Relationship between topography and tendon organ–motor unit interactions in cat tibialis posterior. *Neuroscience Abstracts* **8**, 445.

REINKING, R. M., STEPHENS, J. A. & STUART, D. G. (1975). The tendon organs of cat medial gastrocnemius: significance of motor unit type and size for the activation of Ib afferents. *Journal of Physiology* **250**, 491–512.

SPEILMANN, J. M. & STAUFFER, E. K. (1983). Anatomical correlates of motor unit/tendon organ (MU/TO) response patterns. *Neuroscience Abstracts* **9**, 863.

STAUFFER, E. K. & STEPHENS, J. A. (1975). The tendon organs of cat soleus: static sensitivity to active force. *Experimental Brain Research* **23**, 279–291.

STEPHENS, J. A., REINKING, R. M. & STUART, D. G. (1975). Tendon organs of cat medial gastrocnemius: responses to active and passive forces as a function of muscle length. *Journal of Neurophysiology* **38**, 1217–1231.

STUART, D. G., GOSLOW, G. E., MOSHER, C. G. & REINKING, R. M. (1970). Stretch responsiveness of Golgi tendon organs. *Experimental Brain Research* **10**, 463–476.

STUART, D. G., MOSHER, C. G., GERLACH, R. L. & REINKING, R. M. (1972). Mechanical arrangement and transducing properties of Golgi tendon organs. *Experimental Brain Research* **14**, 274–292.

TELLO, J. (1917). Genesis de las terminaciones nerviosas motrices sensitivas. *Trabajos del Laboratorio de investigaciones biologicas de la Universidad de Madrid* **15**, 101–199.

WINDHORST, U. (1978). Considerations on mechanisms of focused signal transmission in the multi-channel muscle stretch reflex system. *Biological Cybernetics* **31**, 81–90.

WINDHORST, U. & MEYER-LOHMANN, J. (1977). The influence of extrafusal muscle activity on discharge patterns of primary muscle spindle endings. *Pflügers Archiv* **372**, 131–138.

ZELENA, J. & SOUKUP, T. (1977). The development of Golgi tendon organs. *Journal of Neurocytology* **6**, 171–174.