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**ABSTRACT:** Innervation ratios were estimated for motor units supplying superficial lumbrical muscles of the cat after assigning units to one of three types, FF/FI, FR, and S, and estimating their axonal conduction velocity, based on published data. Similarly, unit tensions were converted to muscle fiber number using published values for specific tension and fiber cross-sectional area. A relation was established between axonal area of cross-section and number of fibers innervated which was matched reasonably well by a model of a branching motoneuron with preterminal diameter of 4.28  $\mu\text{m}$  and a daughter-to-parent ratio of 1.48 at each level of branching. It is proposed that the main features of the model are likely to apply to all motoneurons.

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## ON THE BRANCHING OF MOTONEURONS

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In considerations of the pattern of innervation of muscles by motoneurons, it has remained an intuitively appealing idea that large motoneurons with their larger-diameter axons supply more muscle fibers than small motoneurons, that is, have a larger innervation ratio. It led Eccles and Sherrington<sup>10</sup> to the concept of “the caliber of the nerve-fiber *caeteris paribus* (other things being equal) bearing relation to its amount of branching.”

The size of a motor unit, expressed as the isometric tension recorded at the tendon, is determined by three factors: the size of the muscle fibers, their specific tension, and the innervation ratio. The larger a muscle fiber, that is, the more contractile material in parallel, the more force it develops. Estimates, for example, for the cat tibialis anterior muscle indicate that for the three classes of motor unit types,<sup>9</sup> fiber cross-sectional areas differ by up to 75%.<sup>5</sup> Differences in motor unit tension attributable to differences in the specific tension, i.e., the tension produced by unit cross-sectional area of fiber, have also been reported to vary widely. A simple explanation to account for differences in specific tension be-

tween muscle fibers is that there are differences in packing density of the myofibrils. It was argued by Burke and Tsairis<sup>8</sup> that, for the cat medial gastrocnemius muscle, specific tension for type S (slow) units was one-third of that for type FF (fast, fatigable) units and one-fifth of that for type FR (fast, fatigue-resistant) units. Such large differences meant that most of the observed differences in motor unit tension could be accounted for in terms of differences in specific tension and there was little left to incorporate the ideas of Eccles and Sherrington.<sup>10</sup>

More recently it has been shown that differences in specific tension are smaller than first thought, of the order of 70% for units in tibialis anterior.<sup>5</sup> This view is supported by the findings from direct measurements on single muscle fibers of identified type of only small differences in specific tension.<sup>15</sup>

While following these discussions, our thoughts recently returned to some observations we had made some years ago.<sup>12</sup> In studies of motor unit properties of the two superficial lumbrical muscles,<sup>3,12</sup> it was noticed that some of the motor axons running in the main, innervating nerve, a branch of the medial plantar nerve, supplied both muscles. It turned out that the nerve entered the first lumbrical (M1), where some axons terminated, while others innervated a number of muscle fibers before continuing on into the second lumbrical (M2), where they terminated. A third group of axons passed through M1 without making contacts to innervate exclusively fi-

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**Abbreviations:** FF, fast, fatigable units; FI, fast, intermediate units; FR, fast, fatigue-resistant units; S, slow units; M1, first superficial lumbrical muscle; M2, second superficial lumbrical muscle

**Key words:** axon; conduction velocity; motoneuron; motor unit; tension  
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bers in M2. What was particularly interesting was that there was a quite strict relationship between the conduction velocity of the innervating axon and the tension developed by a motor unit. The conduction velocity–tension relation for motor units distributed across both muscles conformed with this relationship only when the tensions generated in the two muscles were added together. It suggested that there was a fixed value for the number of muscle fibers innervated by an axon with a given conduction velocity, regardless of whether the muscle fibers all lay in one muscle or were distributed across both muscles. In other words, it suggested that innervation ratio played an important role in establishment of the conduction velocity–tension relationship. Here we have reexamined our data on motor unit tensions and have explored possible underlying factors that govern the sizes of the units.

## METHODS

Details of the methods have been given in Emonet-Dénand et al.,<sup>12</sup> and only a summary is given of the important points.

All experiments were carried out with approval of the local ethics committee. Cats were deeply anesthetized with pentobarbitone sodium (Nembutal; Rhone Merieux, Pinkenba, Queensland, Australia), 40 mg/kg, supplemented when necessary, during the course of the experiment, with small additional doses. They were killed at the end of the experiment with an overdose of anesthetic.

The superficial lumbrical muscles of the left hind-limb were exposed, together with their common nerve supply, a branch of the medial plantar nerve. When, on occasion, an additional branch was present supplying the second muscle, this was cut. There were always only two muscles, the first (M1) situated medial to the common plantar ligament and inserting on the third digit. The second (M2) lay lateral to the common plantar ligament and inserted on the fourth digit. The distal tendons of each muscle were attached to an isometric myograph. The muscle preparation was enclosed in a perspex box filled with Ringer-Locke solution.

A laminectomy was carried out to expose lumbosacral ventral roots. These were cut at their point of entry into the spinal cord. The hind-limb was extensively denervated, sparing the nerve supply to the lumbrical muscles. Functionally single motor axons were prepared in filaments of ventral root. These were stimulated while recording tension in M1 or M2. Measurements were made of axonal conduction velocity, twitch tension, and time to peak and tetanic tension. Conduction velocity was calculated from the

arrival time in the common lumbrical nerve of the unitary action potential in response to stimulation of the fragment of ventral root. The distance between stimulating and recording electrodes was measured by exposing the sciatic nerve along its entire length and measuring the length of a moist tread placed on top of the nerve along its course. Tension measurements were made at a length corresponding to the whole-muscle optimum for a contraction. On occasions where the axon supplied both M1 and M2, measurements were made first on one muscle, then on the other. Controls were carried out to ensure that there was no cross-transmission of tension between muscles.

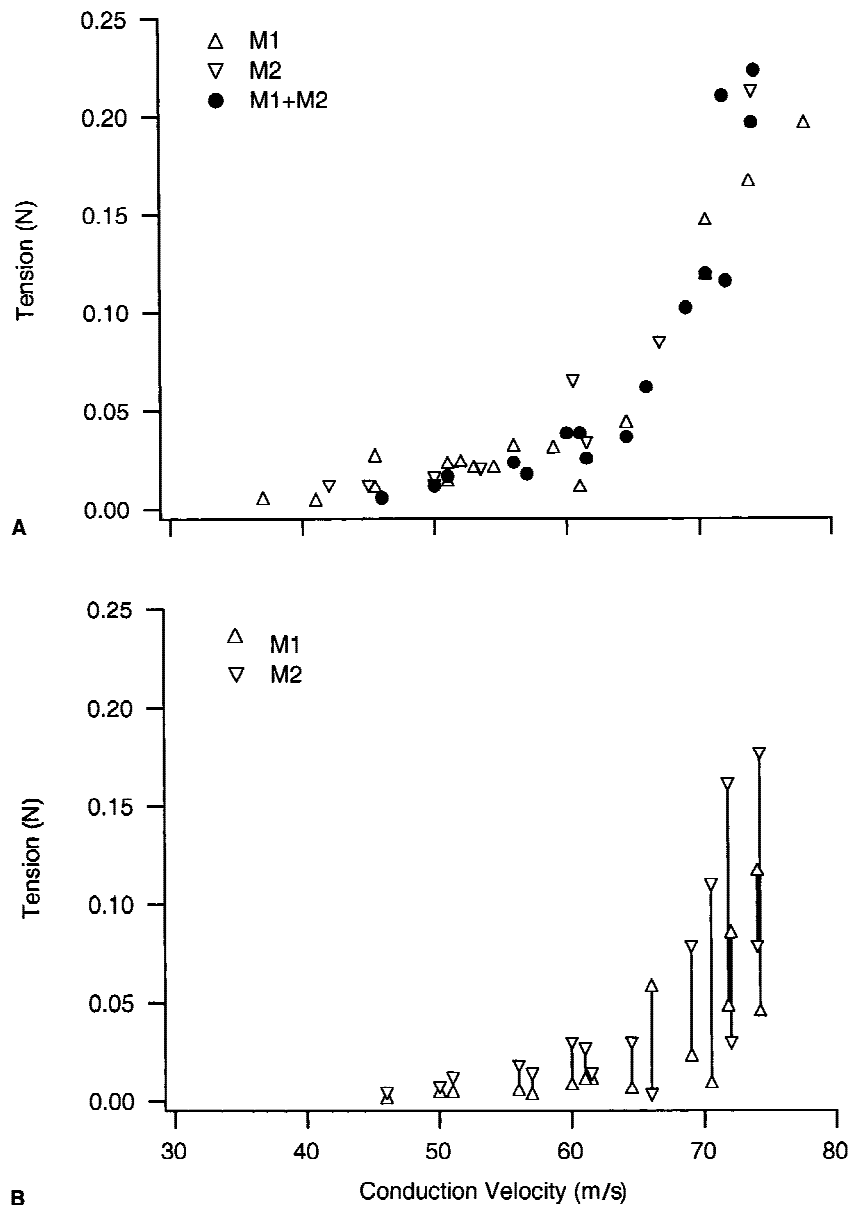
Statistical analysis was carried out on the data for the relation between  $\log_{10}$  tension and estimated axonal areas of cross-section (Fig. 2). A regression line was fitted to the data and residuals calculated. T-tests were used to determine significance of deviations of values from the line. Modeling of axonal branching and the fitting of parameters to the model was done using the program Igor (Wavemetrics, Lake Oswego, Oregon). The fitting algorithm used was a least squares minimization.

## RESULTS

In the original study, observations were made on 218 motor units from eight animals. Descriptions were given of unit contraction speeds and their relation with axonal conduction velocity. It was found that when a motor axon branched to innervate muscle fibers in both muscles, the contraction time courses in the two muscles were almost exactly the same. It emphasized that although fibers belonging to the motor unit lay in separate muscles, they remained under the influence of the one motoneuron.

**Conduction Velocity–Tension Relation.** In this report, we focus attention on the relationship between motor unit tetanic tension and axonal conduction velocity, illustrated in Figure 6 of the original publication and shown, replotted, in Figure 1. The data for this experiment all came from one animal in which M1 generated 0.7N, and M2 generated 0.8N, tetanic tension. The advantage of restricting analysis of data to one animal is that it avoids any potentially confounding influences from interanimal differences. However, a similar relation, a little less clearly delineated, applied to the whole population of motor units studied.<sup>12</sup> Recordings in this one experiment were made from a total of 41 motor units of which 16 supplied M1 only, 9 supplied M2 only, and 16 supplied muscle fibers in both muscles.

The relationship between motor unit tetanic ten-



**FIGURE 1. (A)** A plot of tetanic tension, in N, against axonal conduction velocity, in m/s, for 41 motor units of the two superficial lumbrical muscles of the anesthetized cat. Upward directed triangles M1, downward directed triangles M2. The filled circles are the sum of tensions for motor units distributed to both M1 and M2. Data replotted from Emonet-Dénand et al.<sup>12</sup> **(B)** The components of tension in M1 and M2 for motor units distributed across both muscles, plotted against conduction velocity of the innervating motor axon. Tensions generated in the two muscles by the one axon are indicated by a line joining a pair of points. Symbols as in upper panel.

sion and axonal conduction velocity for the 41 units is shown in Figure 1A. The tension in M1 and M2 for the motor units which were distributed across both muscles have been added together. It can be seen that all values lie on the one relationship, approximately exponential in shape. Importantly, where axons innervated muscle fibers in both muscles, the sum of the tensions from the two muscles closely corresponded to the tension of units with the same axonal conduction velocity but which were restricted to one or other muscle. For the 16 distributed units,

the two components of tension which made up the sum are shown in Figure 1B. For each motor unit, the two values are joined by a line to indicate that the tension is generated by branches of the same axon. It can be seen that the differences between the two components become larger when the innervating axon has a higher conduction velocity. However, when differences are expressed as a percent of the combined tension, there is no systematic trend.<sup>12</sup>

One systematic difference that did emerge was that where axons supplied muscle fibers in both

muscles, the portion in M1 often generated less tension than that in M2. Of the 16 distributed units studied, the tension generated in M2 was greater than that in M1 for 13 of them.

In Figure 1, the slowest axonal conduction velocity for a fiber supplying both muscles was 46 m/s. There were six motor units with axons conducting at less than 46 m/s and these were all restricted to one or other muscle. The same finding was made for the pooled data from all animals.<sup>12</sup> Of the total of 218 motor units isolated, 14 had axonal conduction velocities below 45 m/s. None of these axons supplied both muscles. This suggested that for an axon to be able to supply both muscles, it needed to be of a minimum size. That, in turn, suggested that the axon had to have a certain branching capacity before it could supply both muscles. All of this suggested that branching capacity, i.e., innervation ratio, was an important factor, consistent with the concept of Eccles and Sherrington.<sup>10</sup> Here, we have converted conduction velocity into estimates of axonal area of cross-section, as an expression of the capacity of an axon to branch. Conduction velocity was converted to axon diameter by dividing by 5.7.<sup>6,13</sup> The relation between cross-sectional area and tension is shown for all 41 units in Figure 2A. The relationship closely resembles that seen in Figure 1. For the units supplying the two muscles, both total tension and the individual components are shown.

Because the relation between tension and cross-sectional area is approximately exponential, the data have been replotted on semilogarithmic scales to convert them into a linear relationship and to bring out low values more clearly (Fig. 2B). A regression line fitted to the data points, which included the sum of tensions for units supplying both muscles as well as units which supplied one muscle or the other exclusively, had a slope of 0.013 and was highly significant ( $r^2 = 92\%$ ). For units distributed to both muscles, the values for  $\log_{10}$  (tension) for the portions supplying M1 and M2 were also calculated (Fig. 2). These values deviated significantly from the regression line ( $P < 0.003$ ).

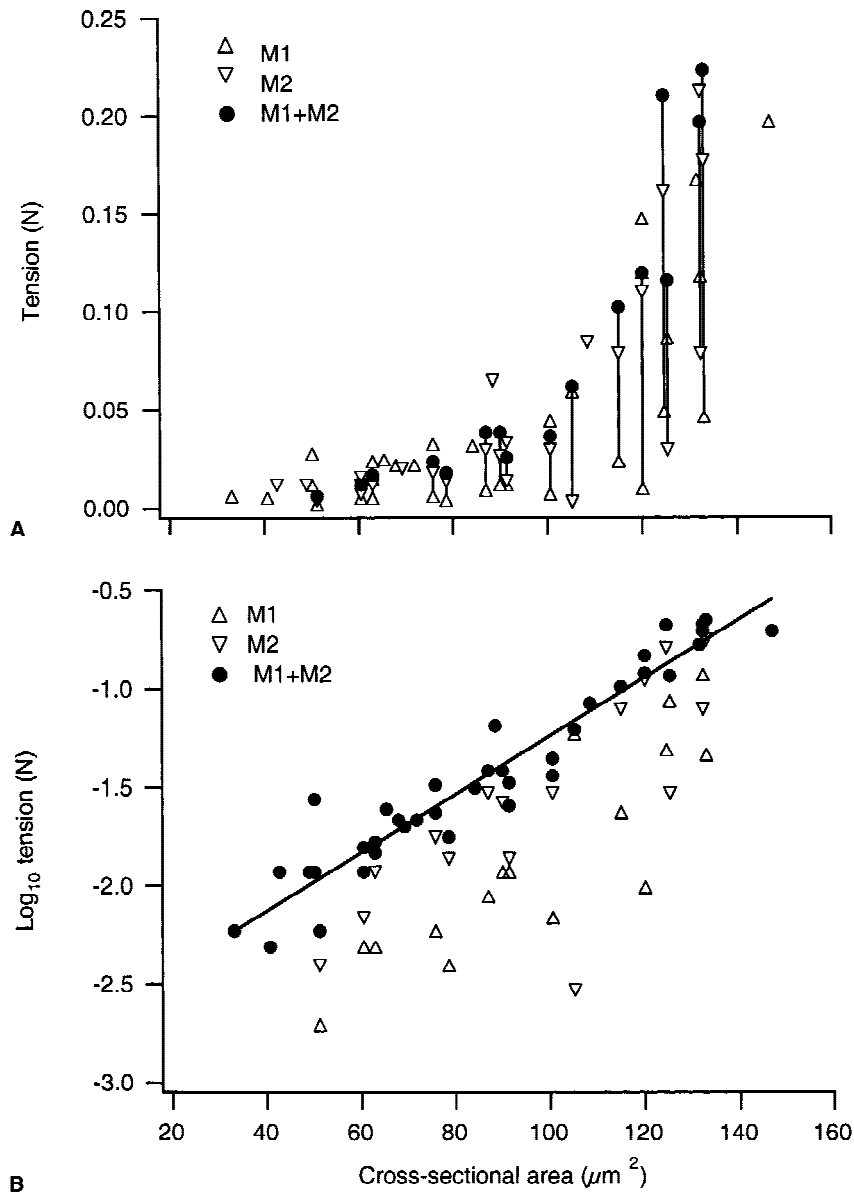
**Modeling.** The strictness of the relation between axonal cross-sectional area and tension encouraged attempts to model the situation using a simple branching model of the motoneuron. In a symmetrically branching structure, if the number of times the axon branches is  $n$ , the number of muscle fibers it will innervate is  $2^n$ . So, for example, if an axon has the capacity to branch six times before its terminals reach a minimum size, it will be able to innervate  $2^6$ , 64 muscle fibers (Fig. 3). To determine an axon's capacity to branch, a key consideration is the rela-

tionship between the size of the parent axon and its daughters. Eccles and Sherrington<sup>10</sup> observed, for axonal branchings in the nerve, that the sum of the daughter cross-sectional areas was 1.05–1.11 times the area of the parent. In other words, the area of each daughter branch was slightly more than half of the parent area.

We began the modeling by making the simplest assumptions. All axon branches at their terminations were assumed to have the same diameters and the sum of the areas of the daughter branches was assumed equal to the parent (ratio of 1.0). All muscle fibers innervated were assumed to generate the same tension so that the recorded tension could be used as a direct expression of fiber number, i.e., the number of terminals supplied by the motoneuron. Both the area of the parent axon and the number of muscle fibers innervated would be proportional to 2 to the power of the number of branchings. That would make area proportional to the number of branchings, and not related exponentially, as observed with the data. However, an important factor that so far has been excluded from consideration is that muscle fibers belonging to different motor units are not likely to generate the same force. Small motor units supplied by slow axons will have smaller muscle fibers than large units.

To take this into account, it was necessary first to assign motor units to one of three types: slow; fast, fatigue-resistant; and fast, fatigable/fast, intermediate (S, FR, and FF/FI). The work of Emonet-Dénand et al.<sup>11</sup> has shown that in superficial lumbricals there are, on average, 64% type S units, 17% type FR, and 19% type FF/FI units. These authors also gave the ranges of conduction velocities covered by the innervating axons (in their Fig. 5). So for the sample of 41 units shown in Figure 1, those with a velocity of 37–62 m/s were assigned to type S (26 units, 63% of the sample). Units in the range 64–72 m/s were assumed to be FR (9 units, 22%), and the remainder (6 units, 15%) were called FF/FI.

Once fiber types were identified, it was possible to estimate the innervation ratio for each motor unit using published values for specific tension (17.2 N/cm<sup>2</sup>, type S; 21.1 N/cm<sup>2</sup>, type FR; 24.9 N/cm<sup>2</sup>, type FF) and for fiber cross-sectional area (2,500  $\mu\text{m}^2$ , type S; 2,400  $\mu\text{m}^2$ , type FR; 3,400  $\mu\text{m}^2$ , type FF).<sup>5</sup> Calculated numbers of muscle fibers for each motor unit, plotted against axonal cross-sectional area are shown in Figure 3. The relation is now less curved than it had been with tension on the ordinate. This is because account has been taken of the fact that muscle fibers for the small units generate

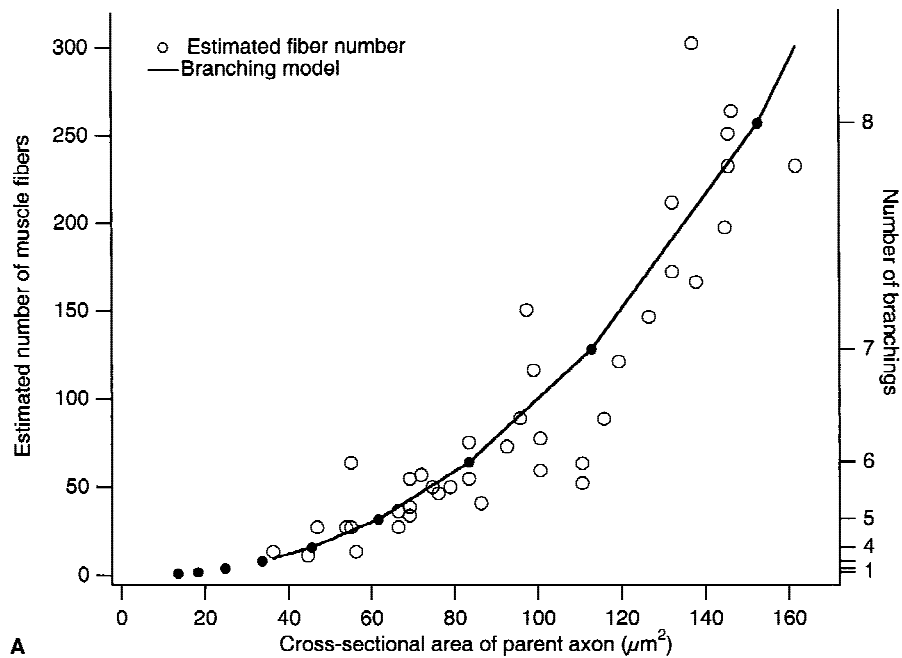


**FIGURE 2. (A)** A plot of tetanic tension for all 41 motor units, including both the tension sum and the individual components for units distributed across both muscles, against estimated motor axon cross-sectional area in  $\mu\text{m}^2$ . Axonal area was calculated from conduction velocity (see text). Symbols as in Figure 1. Lines have been drawn joining the two components of tension and the total for each unit distributed to both muscles. **(B)** A plot of  $\log_{10}$  tension against estimated axonal cross-sectional area for the 41 motor units. Filled circles, values for motor units restricted to one or other muscles and for the sum of tensions for the units distributed to both muscles. Triangles, the components of tension in M1 and in M2 for the distributed units. A regression line has been fitted to the data represented by the filled circles.

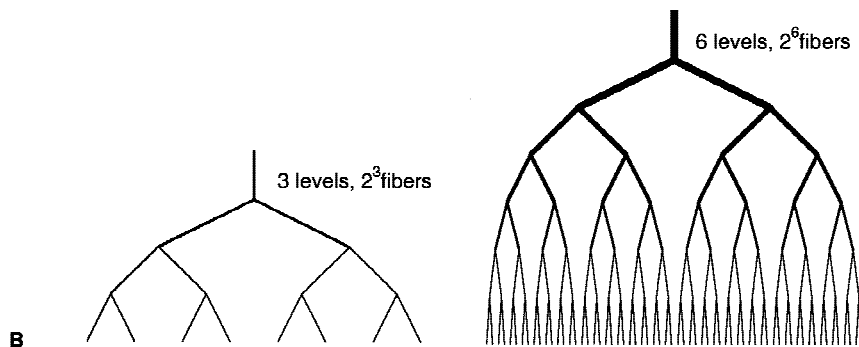
less tension so that calculated numbers are correspondingly larger. In other words, the relation between axonal area and muscle fiber number is not exponential.

Modifying our branching model by allowing the branching ratio to be greater than unity and fitting the model to the values in Figure 3, using branching ratio and terminal size as variables, gave an optimal fit with a ratio of  $1.48 (\pm 0.06)$  and terminal diameter of  $4.28 (\pm 0.05) \mu\text{m}$ .

However, anatomical data suggests that the external internodal diameters of preterminal intramuscular branches of skeletomotor axons is  $2\text{--}4 \mu\text{m}$ .<sup>1</sup> When the model was constrained by a  $3 \mu\text{m}$  diameter terminal axon, it yielded an optimal branching ratio of  $1.35 (\pm 0.005)$  and this still gave a reasonable fit to the data, with the error increased by 25%. More recent published values for branching ratios, measured within the muscle itself, were higher than the 1.1 reported by Eccles and Sherrington.<sup>10</sup> In a study



**A**



**B**

**FIGURE 3. (A)** Relation between axonal area of cross-section and estimated numbers of muscle fibers for each motor unit. The conversion of tension to fiber number required assigning types to motor units using the data of Emonet-Dénand et al.<sup>11</sup> For each unit, tension was converted to fiber number using the average force per cross-sectional area and fiber size for that unit type, cited by Bodine et al.<sup>5</sup> Axonal conduction velocities were assigned, based on the distribution given by Emonet-Dénand et al.<sup>11</sup> The filled circles, joined by lines, represent the calculated relation between axon area and fiber number for a symmetrically branching motoneuron that gave the best fit to the data. The axis on the right gives the number of levels of branching for each point. Terminal branches were assumed to have areas of  $14.4 \mu\text{m}^2$  (diameter  $4.28 \mu\text{m}$ ) and each point represents a different level of branching from 0–8. So an axon with 3 levels of branching innervates 8 muscle fibers, one with 6 levels innervates 64 fibers. A ratio of 1.48 between daughter and parent branch areas was assumed at each branch point, to arrive at a final value of area for the stem axon. **(B)** Examples of branching trees with 3 and 6 levels of branching. Notice the resulting difference in size of the parent axon for the same-sized terminal branches. For further details, see text.

concerned predominantly with the question of the innervation of muscle spindles by skeletomotor axons, Adal and Barker<sup>2</sup> traced the intramuscular branches of motor axons. For the muscle M2, for example, they showed a total of 17 branches with branching ratios ranging from 0.9 to 1.5. The average was 1.27.

#### DISCUSSION

The main purpose of this reevaluation of previously published data was to use it to revisit the question of

the importance of the innervation ratio in determining motor unit tension. The cat lumbrical muscles are particularly interesting because of the well-known, strict relationship between axonal conduction velocity and tension of motor units. Yet the lumbrical muscles contain representatives of all three motor unit types<sup>11,18</sup> so that this is not achieved at the expense of a limited fiber type distribution.

The feature of the superficial lumbricals that we wanted to focus attention on is that the innervating nerve contains motor axons with three distinct pat-

terns of terminations. Some axons terminate in M1, some continue on through M1 into M2 without making any terminations in M1, and some innervate muscle fibers in both muscles. In our original work,<sup>12</sup> we pointed out that for units distributed to both muscles, the two tensions had to be summed for the relation between conduction velocity and tension to be upheld. The precision with which these summed units conformed to the overall relation emphasized its strictness. To bring this out more clearly, we have plotted  $\log_{10}$  tension against estimates of axonal cross-sectional area, representing an expression of an axon's capacity to branch. The closeness of fit of the data to the regression line (Fig. 2) supports the existence of a significant relationship.<sup>4</sup> Furthermore, values lay significantly off the line for portions in one muscle of units distributed to both, implying that these values did not conform with the relationship.

It was the precision with which the split motor units conformed with the conduction velocity:tension relationship that encouraged us to try to model the situation. We considered a simple branching model of the motoneuron and soon realized that this would not generate an exponential relationship between axonal cross-sectional area and tension. As a first step towards achieving a better fit to the data, we converted tension for each motor unit into numbers of muscle fibers, using published values for specific tension and fiber size.<sup>5</sup> It should be pointed out that these data come from the much larger tibialis anterior muscle so that the values may not be quite correct for the lumbricals. Nevertheless, a reasonable relationship was established between fiber number and axonal conduction velocity, converted to axonal area (Fig. 3). When a branching model was fitted to this data, the best fit was achieved with a terminal diameter of 4.28  $\mu\text{m}$  and branching ratio of 1.48 (Fig. 3). This compares with reports from anatomical studies of terminal diameters of 2–4  $\mu\text{m}$ <sup>1</sup> and mean intramuscular branching ratios of 1.27.<sup>2</sup>

In their study of skeletomotor and fusimotor innervation of spindles in deep lumbrical muscles of the cat, Adal and Barker<sup>2</sup> estimated skeletomotor innervation ratios for axons with diameters in the range 7.5–13.5  $\mu\text{m}$  (mean 12.6  $\mu\text{m}$ ) as 1:260–1:300. From Figure 3, our estimate for an axon 13.5  $\mu\text{m}$  in diameter (143  $\mu\text{m}^2$  area, 77 m/s conduction velocity) lies in the range 1:190–1:260, so fits their data reasonable well, given the many assumptions made in these calculations.

Estimates of muscle fiber numbers for axons in the conduction velocity range of 37–45 m/s (area 33  $\mu\text{m}^2$ –49  $\mu\text{m}^2$ ) were 11–63. This therefore represents

the lower end of the useful range for motor units distributed to both muscles, because axons with a conduction velocity below 45 m/s supplied only one or other muscle exclusively. So the smallest non-branching unit had 11 fibers which compares with an estimate of 4 fibers for the smallest part-unit. It suggests that restraint on size does not apply to part-units. That, in turn, suggests that the units distributed to both muscles adopt their place in the recruitment order according to the combined tensions from the two muscles, not the part-tension in one muscle.

Closer inspection of the data of Adal and Barker<sup>2</sup> shows that there is no identifiable trend in the distribution of branching ratios for the portion of the tree that has been traced (their Fig. 1). Intuitively it might have been expected that the ratio would fall as more peripheral terminals were reached, i.e., that there was less loss in diameter for peripheral terminals than for the primary branches. This did not seem to be the case. However, it should be remembered that Adal and Barker were primarily concerned with the motor supply of spindles and that only 17 of the approximately 300 terminals were measured. Given the strictness of the relationship between axon size and tension in the lumbrical muscles, it seems unlikely that, for these muscles, branching ratios were entirely randomly distributed. The point should be pursued in future anatomical studies. Attempts should be made to obtain ratios for branches throughout the tree and to determine whether any consistent trends can be revealed in their distribution.

In our modeling studies, we explored the consequences of changing the branching ratio, increasing its value for more peripheral branchings. This did not lead to a significant improvement in the goodness-of-fit (Chi-squared reduced by less than 10%) and yielded a coefficient that was not significantly different from zero.

In the original study, properties of a total of 218 motor units from eight animals were examined. Of the sample, 47% had axons that innervated muscle fibers located only in M1, 27% supplied only M2, and 27% supplied both. The data suggested that about one-half of the axons supply M1, one-quarter supply M2, and one-quarter supply both muscles. Yet the tensions developed by the two muscles are about the same. The potential shortfall of motor units in M2 is made up in two ways. First, in some animals, M2 received an additional independent nerve branch from the lateral plantar nerve.<sup>12</sup> For the purposes of our experiments, this branch, when present, had been cut. The second factor was that for two-

thirds of the units distributed across the two muscles, the component in M2 developed more tension than that in M1. For animals with no separate nerve to M2, it meant that, in M2, the same whole muscle tension was achieved by a smaller number of motor units. Why this difference occurs in pattern of innervation remains uncertain. Perhaps, during development, there is competition between the outgrowing axons for target muscle fibers, and axons that are unable to find sufficient available terminals in M1 make up most of their complement in M2.

It remains to consider to what extent the propositions presented here can be applied to other muscles. The conduction velocity–tension relation for larger muscles, like medial gastrocnemius of the cat, does not show as clear a trend as for the lumbrical muscles,<sup>7,17,19,20</sup> although, if consideration is restricted to fatigue-resistant motor units, a significant relation emerges.<sup>11</sup> It appears that some of the larger, type FF units develop more tension than predicted from the relation with axonal conduction velocity. Perhaps, for these units, factors other than innervation ratio have become predominant, such as fiber size.<sup>5</sup> It is known that there is exercise-dependent conversion of fiber types.<sup>14</sup> Such conversions might be expected to blur the original underlying relationship. However, for cat flexor digitorum longus, Bagust et al.<sup>4</sup> were able to fit their motor unit data with a regression line obtained from the data of Emonet-Dénand et al.,<sup>12</sup> and they concluded that the relationship between conduction velocity and tension must have a wide significance.

Based on our findings, we conclude that an axon's capacity to branch is an important determinant of the amount of tension developed by the motor unit. While for some muscles the strictness of this relationship is partly confounded by other factors, such as fiber type conversions, its essential features are likely to apply to motoneurons of all muscles. Recognition of this fact raises the question of why it should be so. One obvious possibility is that larger axons are able to transport more materials from the soma to the terminals and therefore are able to support a larger number of terminals. It implies that there are limits to the sizes of normal motor unit territories and those established after injury,<sup>21</sup> or as a result of motoneuron loss during aging.<sup>16</sup>

Why should the two superficial lumbrical muscles have motor units common to both muscles? Presumably, for some functions, the two muscles are activated as one, whereas for others, they are activated independently. Whatever the reason, the presence of such distributed units allows recognition of the strictness of the relation between the size of an axon

and the number of muscle fibers it innervates. That, in turn, reinforces the view that an important determinant of a motor unit's size is its innervation ratio.

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