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Skeletal Muscle Architecture of the Rabbit Hindlimb: Functional Implications of Muscle Design

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ABSTRACT The muscle-fiber architecture of 29 muscles from six rabbits (*Oryctolagus cuniculus*) was measured in order to describe the muscular properties of this cursorial animal, which possesses several specific skeletal adaptations. Several muscles were placed into one of four functional groups: hamstrings, quadriceps, dorsiflexors, or plantarflexors, for statistical comparison of properties between groups. Antagonistic groups (i.e., hamstrings vs. quadriceps or dorsiflexors vs. plantarflexors) demonstrated significant differences in fiber length, fiber length/muscle length ratio, muscle mass, pinnation angle, and number of sarcomeres in series ($P<.02$). Discriminant analysis permitted characterization of the "typical" muscle belonging to one of the four groups. The quadriceps were characterized by their large pinnation angles and low fiber length/mass ratios, suggesting a design for force production. Conversely, the hamstrings, with small pinnation angles, appeared to be designed to permit large excursions. Similar differences were observed between plantarflexors and dorsiflexors, which have architectural features that suit them for force production and excursion respectively. Although these differences were not absolute, they represented clear morphological distinctions that have functional consequences.

Skeletal muscle contractile properties are a function of both the intrinsic muscle fiber properties and the fiber arrangement within the muscle (i.e., the architectural design). While the specific tension and contractile speed of fast and slow fibers may differ by about a factor of two (Close, '72; McDonagh et al., '80; Burke, '81; Powell et al., '84; Bodine et al., '87), the difference in strength and speed between muscles of different architecture is much greater (Gans, '82; Wickiewicz et al., '83; Powell et al., '84; McClearn, '85). Architectural analysis of limb muscles from cats (Spector et al., '80; Goslow et al., 1981; Bodine et al., '82; Sacks and Roy, '82; English, '84; Loeb et al., '87), guinea pigs (Powell et al., '84), humans (Wickiewicz et al., '83), and monkeys (Roy et al., '84) has provided a conceptual framework around which to address the question of skeletal muscle design and neuromotor control.

Previous muscle architectural studies have been performed on muscles taken from a number of different individual animals. As a result of interanimal variability, it has been difficult to make detailed quantitative comparisons between muscle groups within an animal. In the present study, all muscles were taken from the same six animals. As a result, we were able, using statistical analysis, to determine the most significant architectural features that discriminated among functional groups within an animal.

Additionally, because a number of specializations of the rabbit skeleton have been reported (Eaton, '44; Howell, '65, Hildebrand, '74), which include deepening of the patellar groove, caudal curvature of the radius and ulna, fusion of the tibia and fibula, proximally placed muscle mass, and modi-

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fication of the shape of the carpal bones, we asked if muscular specializations might also occur to complement the skeletal adaptations.

The objectives of this study, therefore, were to quantitatively characterize the muscle fiber architecture of the rabbit hindlimb in order to elucidate morphological differences between functional groups and to investigate whether the muscular and skeletal specialization might complement one another.

MATERIALS AND METHODS

Muscles were dissected from the hindlimbs of six New Zealand White rabbits (*Oryctolagus cuniculus*) with an average mass of 2.5 ± 0.2 kg (mean ± SD). After sacrifice, animals were skinned, transected at the sacrum, and fixed for 3–5 days in 10% buffered formalin with hips, knees, and ankles held in 90° of flexion and abduction (chosen arbitrarily) for architectural determination, according to the methods of Sacks and Roy ('82), except that the partial digestion in H_2SO_4 was omitted. Individual muscles were carefully isolated and removed, blotted dry, and weighed (WT). Muscle length (ML) was measured with a dial caliper as the distance from the origin of the most proximal muscle fibers to the insertion of the most distal fibers. Surface fiber pinnation angle was estimated in the proximal, middle, and distal muscle region with a dissecting microscope and goniometer. Fiber bundles consisting of 5–15 fibers were teased from the proximal, middle, and distal region of each muscle. Fiber bundle length (FL) was measured in each region, and bundles were mounted on slides for sarcomere length determination according to Lieber et al. ('84). Note that in the present study, FL values do not actually refer to a single, anatomically distinct muscle fiber (cf. Loeb et al. '87) but are used as a shorthand term for the origin-to-insertion distance along the line of fiber pinnation.

Mean sarcomere length (SL) and fiber length were calculated for each muscle. Muscle length and fiber length were normalized to a sarcomere length of 2.2 μm to enable comparison between muscles by eliminating variability resulting from differences in joint fixation angle (Sacks and Roy, '82). Physiological cross-sectional area (CSA) was calculated by the equation

$$\text{CSA} = \frac{(\text{muscle mass}) \cdot \cos \theta}{(\text{fiber length}) \cdot 1.054}$$

where 1.054 g/cm^3 was used for the density of skeletal muscle (Mendez and Keys, '60) and θ represents the average pinnation angle. Data were expressed as the ratio of FL/ML, the more highly pinnated muscles having a lower ratio. In addition, for each muscle, the ratio FL/WT was calculated as an index representing a design tendency toward muscle excursion; and CSA/WT was calculated as an index representing a design tendency toward muscle force. It should be noted that muscle fiber architecture alone does not permit deduction of physiological design tendency. For example, as explained by Gans and de Vree ('87), an increase in sarcomere number may represent an adaptation for high-velocity movement or may simply allow a muscle to generate large forces in spite of high velocities. Because detailed analysis of moment arms was not attempted in the present study, FL/WT and CSA/WT will be presented as design tendencies, assuming roughly equivalent moment arms. Calculations were performed for each muscle and for each functional muscle group (see below).

For gross comparisons between selected functional groups, muscles were lumped into four groups: quadriceps, hamstrings, plantarflexors, and dorsiflexors. Quadriceps muscles included the rectus femoris (RF), vastus medialis (VM), vastus lateralis (VL), and vastus intermedius (VI). Hamstrings included the semimembranosus (SM, proximal and distal portions), semitendinosus (ST, proximal and distal heads), and biceps femoris (BIC, long head only). Ankle dorsiflexors included the tibialis anterior (TA), extensor digitorum longus (EDL), peroneus brevis (PB), peroneus tertius (PT), and peroneus longus (PL). Ankle plantarflexors included the medial gastrocnemius (MG), lateral gastrocnemius (LG), soleus (SOL), plantaris (PLA), tibialis posterior (TP), flexor digitorum longus (FDL), and flexor hallucis longus (FHL). The architecture of other muscles was determined and is shown in the figures, but values from these muscles were not included in the statistical comparisons between groups, because of uncertainty regarding function. Other muscles characterized included the adductor longus (AL), adductor magnus (AM), adductor brevis (AB), pectinius (PEC), gracilis (GRA), popliteus (POP), and tensor fascia latae (TFL). It was not possible to clearly dissect the sartorius muscle from the rabbit.

Moment arm for the ankle plantarflexors (MG, LG, SOL, PLA) was measured as the

distance between the achilles tendon insertion on the calcaneus to the estimated center of the ankle joint (at the level of the malleoli). The moment arm for the TA was measured as the distance from the TA insertion at the base of the first metatarsal to the estimated center of the ankle joint. The EDL moment arm was measured as the distance from the EDL insertion at the third distal interphalangeal (DIP) joint to the ankle center.

Statistical analysis

Mean sarcomere length and fiber lengths were compared between proximal, middle, and distal regions for each muscle with one-way analysis of variance (ANOVA, BMDP Program P1V) (Dixon, '83). In addition, for each parameter, muscles were lumped into functional groups, i.e., hamstrings, quadriceps, dorsiflexors, and plantarflexors, and an ANOVA was performed between antagonistic groups. To address the question as to whether muscles were designed preferentially for force or excursion, FL/WT was regressed on CSA/WT with simple linear regression (BMDP Program P1R) (Dixon, '83). Finally, in order to determine which of the measured parameters most significantly distinguished between functional groups, discriminant analysis (BMDP Program P7M) (Dixon, '83) was performed among all four functional groups and then between antagonists, i.e., hamstrings vs. quadriceps and dorsiflexors vs. plantarflexors, with F-to-enter = 3.000 and F-to-remove = 2.996. In all cases, statistical results were considered significant for $P<.05$.

RESULTS

General features

Most architectural features (Table 1) of the rabbit hindlimb muscles were similar to those observed in the cat (Sacks and Roy, '82), and guinea pig (Powell et al., '84). The notable exception was the SOL, which had relatively shorter fibers (Fig. 1) and a lower FL/ML ratio (Fig. 2), compared with cats and guinea pigs, but was very similar to that observed in humans (Wickiewicz et al., '83). The muscle with the longest fibers was the AM (FL = 69.5 mm), whereas the muscle with the shortest fibers was the POP (Fl = 8.5 mm). The muscle with the most longitudinally arranged fibers was the AL (FL/ML ratio = 0.83); the muscle with the smallest FL/ML ratio was the PT (ratio = 0.18). The most highly pinnated muscle was the VI (angle = 20°); the least pinnated muscle was the GRA (angle = 0°). The largest muscle by far was the BIC (mass = 37.2 g); the smallest was the PL (mass = 0.65 g).

Comparisons between functional groups

When muscles were grouped functionally, a significant difference was observed between quadriceps and hamstrings for FL ($P<.0001$, Fig. 1), FL/ML ratio ($P<.0001$, Fig. 2), muscle mass ($P<.02$), pinnation angle ($P<.0001$, Fig. 3), and number of sarcomeres in series ($P<.001$). For the dorsiflexors vs. plantarflexors comparison, a significant difference was observed for muscle FL ($P<.02$, Fig. 1), FL/ML ratio ($P<.01$, Fig. 2), muscle mass ($P<.0002$), pinnation angle ($P<.0002$, Fig. 3), CSA ($P<.0001$, Fig. 4), and number of sarcomeres in series ($P<.02$). Thus, the only parameter that was significantly different for dorsiflexors vs. plantarflexors but not for hamstrings vs. quadriceps was CSA (Fig. 4). No significant SL difference was observed between proximal, middle, and distal portions of the muscle ($P>.5$).

Discriminant analysis revealed that the parameter that best discriminated between all four functional groups was FL/WT, followed by WT, CSA/WT, pinnation angle, and number of sarcomeres in series. The four functional groups thus differed in a number of intrinsic properties, not just absolute size. With these parameters and the discriminating function, it was possible to retrospectively classify 65% of the muscles correctly as either quadriceps, hamstrings, dorsiflexors, or plantarflexors. Individually, the easiest groups to classify were, in order, quadriceps (71%, 17/24), dorsiflexors (67%, 20/30), hamstrings (67%, 12/18), and plantarflexors (60%, 25/42). The discriminating function therefore correctly classified the muscles almost three times better than would have been obtained by chance. Interestingly, the six hamstring muscles that were incorrectly classified were STs, and they were classified as plantarflexors (2/6) or dorsiflexors (4/6) rather than hamstrings. The misclassified ST thus more closely resembled shank muscles than thigh muscles. Similarly, of the ten dorsiflexors incorrectly classified, one-half (5/10) were the EDL, incorrectly classified as a plantarflexor.

When considering only the muscles of the thigh, i.e., discriminating only between hamstrings and quadriceps, the best discriminators were, in order, WT, FL/WT, FL/ML, and CSA/WT. It was possible ret-

TABLE 1. Architectural features of the rabbit hindlimb[1]

Muscle Studied	Fiber Length (mm)	Cross-Sectional Area (cm^2)	FL/ML ratio	Sarcomere length (μm)
Gastrocnemius				
Medial (MG)	14.69 ± 0.67	2.99 ± 0.36	0.24 ± 0.01	2.29 ± 0.10
Lateral (LG)	16.06 ± 0.76	3.77 ± 0.09	0.28 ± 0.01	2.35 ± 0.03
Soleus (SOL)	13.81 ± 0.80	1.07 ± 0.08	0.24 ± 0.01	2.29 ± 0.07
Plantaris (PLA)	12.70 ± 0.65	3.04 ± 0.19	0.18 ± 0.01	2.25 ± 0.09
Tibialis posterior (TP)	10.69 ± 1.24	0.71 ± 0.11	0.23 ± 0.01	2.52 ± 0.08
Flexor digitorum Longus (FDL)	12.35 ± 0.52	1.19 ± 0.15	0.24 ± 0.02	2.29 ± 0.12
Flexor hallucis Longus (FHL)	12.03 ± 0.47	1.37 ± 0.17	0.19 ± 0.02	2.29 ± 0.13
Plantarflexors (n = 42)[2]	13.19 ± 0.37	2.03 ± 0.19	0.23 ± 0.01	2.32 ± 0.04
Tibialis anterior (TA)	38.08 ± 3.00	0.59 ± 0.04	0.67 ± 0.02	2.48 ± 0.11
Extensor digitorum Longus (EDL)	15.34 ± 1.33	1.42 ± 0.12	0.23 ± 0.01	2.45 ± 0.09
Peroneus longus (PL)	12.41 ± 0.86	0.50 ± 0.05	0.30 ± 0.02	2.44 ± 0.04
Peroneus brevis (PB)	12.71 ± 1.01	0.53 ± 0.09	0.32 ± 0.04	2.44 ± 0.11
Peroneus tertius (PT)	9.27 ± 0.62	0.70 ± 0.10	0.18 ± 0.01	2.37 ± 0.12
Dorsiflexors (n = 30)	17.57 ± 2.05	0.75 ± 0.07	0.34 ± 0.03	2.44 ± 0.04
Biceps femoris (BIC)	41.10 ± 5.51	9.49 ± 1.55	0.41 ± 0.05	2.23 ± 0.08
Semimembranosis (SMP)	48.28 ± 2.15	1.93 ± 0.17	0.67 ± 0.01	2.29 ± 0.10
Semitendinosis (ST)	20.22 ± 1.46	0.81 ± 0.06	0.37 ± 0.02	2.68 ± 0.03
Hamstrings (n = 18)	36.53 ± 3.46	4.08 ± 1.06	0.49 ± 0.04	2.40 ± 0.06
Rectus femoris (RF)	16.28 ± 1.56	3.95 ± 0.53	0.21 ± 0.02	2.23 ± 0.12
Vastus lateralis (VL)	29.64 ± 2.89	4.00 ± 0.52	0.39 ± 0.03	2.28 ± 0.05
Vastus medialis (VM)	18.92 ± 1.83	2.75 ± 0.26	0.30 ± 0.03	2.47 ± 0.03
Vastus intermedius (VI)	19.10 ± 1.54	3.40 ± 0.44	0.29 ± 0.02	2.36 ± 0.07
Quadriceps (n = 24)	20.99 ± 1.43	3.53 ± 0.24	0.30 ± 0.02	2.34 ± 0.04
Pectineus (PEC)	12.39 ± 0.64	0.73 ± 0.11	0.47 ± 0.04	3.23 ± 0.30
Adductor brevis (AB)	13.44 ± 2.35	0.65 ± 0.13	0.39 ± 0.03	2.68 ± 0.16
Adductor magnus (AM)	69.54 ± 8.28	2.98 ± 0.40	0.81 ± 0.09	2.46 ± 0.07
Adductor longus (AL)	54.79 ± 3.55	2.32 ± 0.14	0.83 ± 0.04	2.71 ± 0.08
Gracilis (GRA)	34.79 ± 5.23	1.70 ± 0.19	0.68 ± 0.12	3.15 ± 0.14
Tensor fascia latae (TFL)	30.41 ± 6.15	2.86 ± 0.52	0.45 ± 0.09	2.03 ± 0.10
Popliteus (POP)	8.51 ± 0.53	1.28 ± 0.07	0.29 ± 0.02	2.42 ± 0.10

[1]Values are presented as mean ± SEM, n = 6, for each muscle studied.
[2]Bold type indicates summarized data for functional groups.

rospectively to classify 100% of the muscles correctly (42/42) with these variables and the discriminating function. Only two variables, FL/WT and pinnation angle, were entered into the equation to discriminate between dorsi- and plantarflexors; when used to retrospectively discriminate between groups, they correctly classified 86% of the plantarflexors (36/42) and 73% of the dorsiflexors (22/30). The fact that more variables were used to discriminate between hamstrings and quadriceps than dorsiflexors and plantarflexors indicated that, overall, the functional groups of the thigh were more "different" than the functional groups of the shank.

Linear regression for the hamstrings demonstrated a significant positive correlation between FL/WT and CSA/WT ($P<.004$, $r = +0.65$), whereas the quadriceps demonstrated a significant negative correlation ($P<.05$, $r = -0.60$). While the regression relationships were not statistically significant for the functional groups of the shank, a similar trend was seen, in that the dorsiflexors demonstrated a negative correlation ($P = .26$, $r = -0.71$), whereas the plantarflexors demonstrated a positive correlation that was nearly significant ($P = .07$, $r = 0.69$). Finally, a significant difference was observed between the various regression relationships obtained for the four functional groups ($P<.00001$).

DISCUSSION

This study demonstrated that the muscular architecture of the rabbit hindlimb is similar to that reported for other mammal-

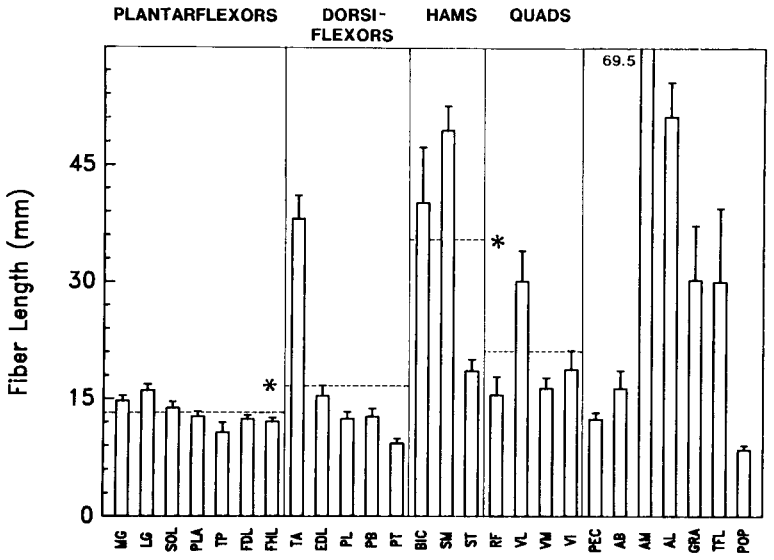

Fig. 1. Muscle fiber length (mm) for 26 muscles of the rabbit hindlimb. Vertical lines represent functional division of muscles in plantarflexors, dorsiflexors, hamstrings, and quadriceps. **Asterisk** represents significant difference ($P<.05$) between antagonists (i.e., plantarflexors vs. dorsiflexors and hamstrings vs. quadriceps), as demonstrated by one-way ANOVA. See Methods for muscle abbreviations.

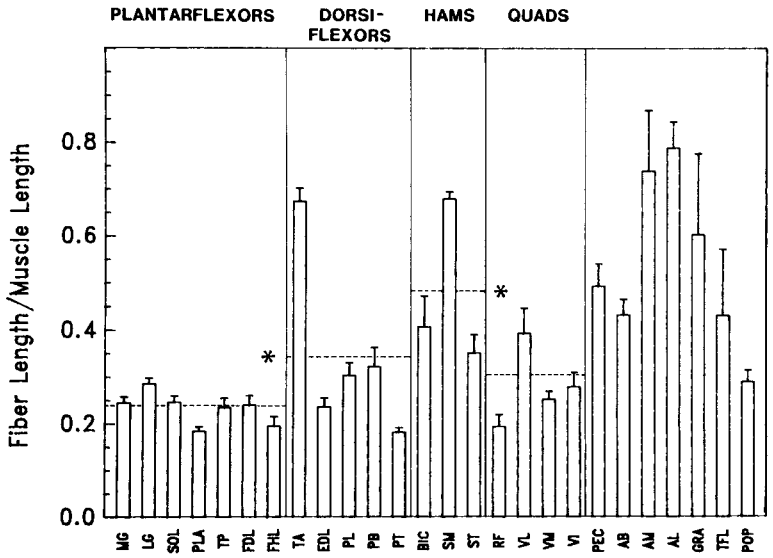

Fig. 2. Fiber length/muscle length ratio for 26 muscles of the rabbit hindlimb. Verticle lines represent functional division of muscles in plantarflexors, dorsiflexors, hamstrings, and quadriceps. **Asterisk** represents significant difference ($P.05$) between antagonists (i.e., plantarflexors vs. dorsiflexors and hamstrings vs. quadriceps), as demonstrated by one-way ANOVA.

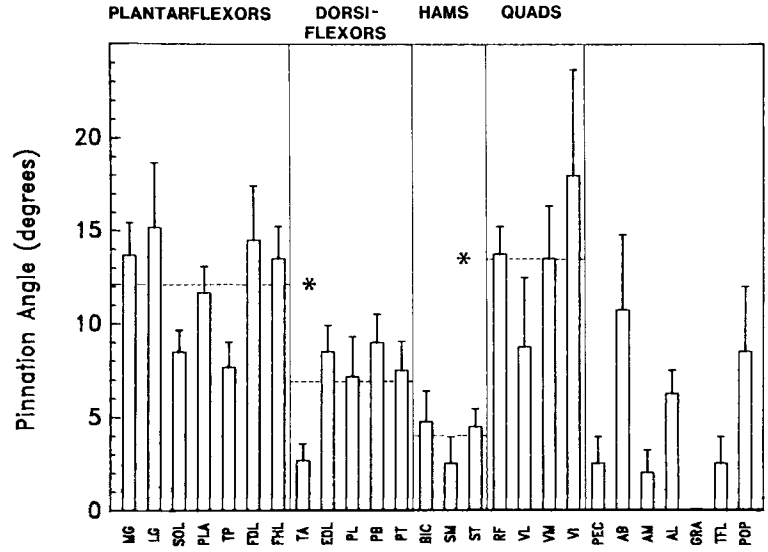

Fig. 3. Pinnation angle (degrees) for 26 muscles of the rabbit hindlimb. Vertical lines represent functional division of muscles in plantarflexors, dorsiflexors, hamstrings, and quadriceps. **Asterisk** represents significant difference ($P<.05$) between antagonists (i.e., plantarflexors vs. dorsiflexors and hamstrings vs. quadriceps), as demonstrated by one-way ANOVA.

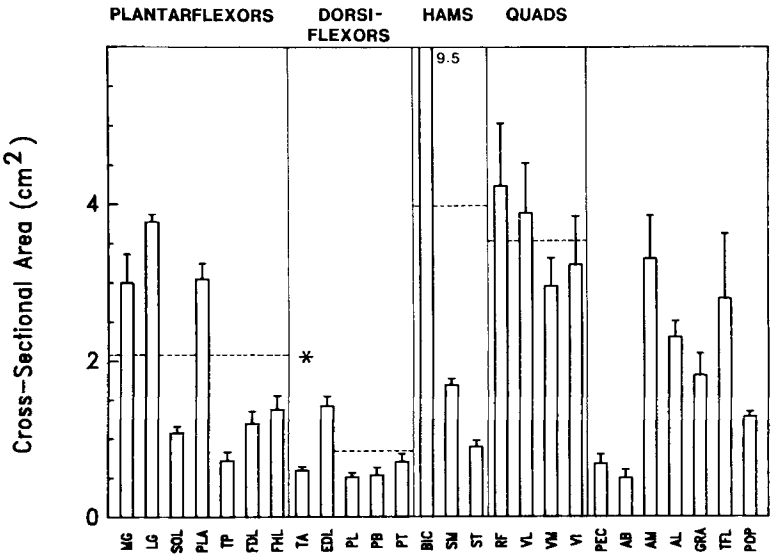

Fig. 4. Physiological cross-sectional area (cm^2) for 26 muscles of the rabbit hindlimb. Vertical lines represent functional division of muscles in plantarflexors, dorsiflexors, hamstrings, and quadriceps. **Asterisk** represents significant difference ($P<.05$) between antagonists (i.e., plantarflexors vs. dorsiflexors and hamstrings vs. quadriceps), as demonstrated by one-way ANOVA. See methods for muscle abbreviations.

ian systems: the cat (Sacks and Roy, '82), guinea pig (Powell et al., '84), and human (Wickiewicz et al., '83). In accordance with previous architectural studies, the data support the notion that the neuromusculoskeletal system is able to perform movement tasks by sending command signals to specialized effector organs whose properties are presumably tailored to the required movement. This simplifies the requirements of the neuromotor controlling signal and permits the precise effect of a given motor input to be "decoded" by the properties of the muscle itself. In addition, although skeletal specializations have been reported for the rabbit, analogous specializations at the level of the muscle were not demonstrated. It appears that the main muscular adaptation for the rabbit as a cursor and saltator is to locate the bulk of the muscle mass proximally, thereby decreasing hindlimb rotational inertia.

This study rules out the possibility, although it would have been considered unlikely a priori, that control of muscle force is accomplished by gross sarcomere length differences between or along the length of muscles. Although longitudinal sarcomere length inhomogeneities have been shown to have a profound influence on the contractile properties of the single fiber (Julian and Morgan, '79, ter Keurs et al., '78; Lieber and Baskin, '83; Altringham and Botinelli, '85), this strategy apparently is not functional as a force modulator in the whole muscle.

Discriminant analysis between the four functional groups and between thigh and shank antagonists elucidated the unique differences between the various muscle groups in terms of design. Several discriminators were intrinsic, i.e., not dependent on the absolute muscle size; others were extrinsic, i.e., dependent on the muscle size. It is interesting to note that of the five best discriminators between all four groups (FL/WT, WT, CSA/WT, angle, number of sarcomeres in series), two of the five are intrinsic properties and the remaining three extrinsic. This indicates that differences between functional groups are not simply size differences but also differences in mass distribution. This combination of intrinsic and extrinsic differences is observed even when discriminating between antagonists. For example, of the four best discriminators between hamstrings and quadriceps (WT, FL/WT, FL/ML, and CSA/WT), one is an extrinsic property, whereas the remaining three are intrinsic. Similarly, when considering dorsiflexors vs. plantarflexors, the three best discriminators (CSA/WT, CSA, and FL/WT) consist of one extrinsic and two intrinsic properties.

With these discriminating parameters, it is possible to describe the "typical" muscle belonging to a functional group. For example, the quadriceps are characterized by their large pinnation angle, moderate size, and low FL/WT ratio, generally designed for force production. The hamstrings, on the other hand, are very large, long muscles composed of longitudinally arranged fibers, with a low CSA/WT ratio designed intrinsically for excursion, but, based on their size, also able to generate large forces. In the shank, dorsiflexors are small muscles with a very high FL/WT ratio and relatively longitudinally arranged fibers, designed for excursion. The plantarflexors, like the quadriceps, are highly pinnated, albeit smaller, with a very high CSA/WT ratio and short fibers. To the extent that the calculated ratios represent the tendency toward force or excursion, therefore, the plantarflexors are clearly designed for force production, whereas the dorsiflexors are clearly designed for excursion. The thigh muscles appear less extremely adapted, with the hamstrings possessing a tendency toward excursion but retaining a good deal of size for adequate force production. Similarly, the quadriceps maintain a tendency toward force production and are less adapted for excursion. Explanation for design tendency must ultimately include information on muscle moment arms.

The question as to whether muscles are designed in terms of force *or* excursion is addressed by inspection of the regression relationships between FL/WT and CSA/WT. In the hamstrings, the muscles are designed for force *and* excursion, whereas in the quadriceps, it is more an either or phenomenon. A similar tendency is seen in the shank, where the plantarflexors appear to be both force and excursion generators, whereas the dorsiflexors appear to be designed for one or the other. In fact, the EDL and TA appear to be a good pair of synergists, with nearly opposite design strategies.

The arguments presented here are stated in terms of muscle force, whereas the mechanical property that is most relevant to movement is the moment generated at the joint of interest (Gans and De Vree, '87). It is possible, for example, that although a muscle is designed for force, if the muscle insertion position creates a small moment

arm, the net result would be a joint with a high angular velocity. Similarly, if the hamstrings and quadriceps possessed identical moment arms about the knee, the quadriceps would generate more tension because of their large cross-sectional area. However, at relatively high angular velocities, the drop in quadriceps force might actually be greater than that of the hamstrings because of the fewer numbers of sarcomeres in series. It was difficult to generalize the overall effect of considering moment arms, except to say that the inclusion of moment arms (and therefore joint torque calculations) did not substantially alter the conclusions presented above. In one case, the comparison was straightforward: the TA was compared to the EDL. Both muscles are dorsiflexors, but it was clear that the TA was designed more for excursion production and the EDL more for force production (Figs. 2–4). Interestingly, the TA moment arm acting at the ankle (2.5 ± 0.2 cm) was less than half of the EDL moment arm (6.2 ± 0.3 cm), suggesting that in terms of joint angular velocity, the force/excursion disparity between the two muscles was actually accentuated. A second comparison was made between four of the plantarflexors (MG, LG, SOL, and PLA) because their common insertion resulted in nearly identical moment arm between muscles. In this case, it appeared that the gastrocnemius was designed for force production, based not on any intrinsic difference between it and the SOL and PLANT (Fig. 2), but simply on its larger mass. This is a situation where Nature has solved the force problem simply by increasing the size of the motor and keeping the mass near the knee joint, thereby maintaining a relatively small moment of inertia.

In summary, the hindlimb muscles of the rabbit are similar to those observed in other mammalian systems, and they provide insights into skeletal muscle design. The numerous observed arrangements of muscle fibers and muscle mass indicate that the production of movement is a complex task that is well coordinated between nerves, muscles, and joints.

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