

Clinical Significance of Skeletal Muscle Architecture

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Skeletal muscle architecture is one of the most important properties that determines a muscle's force and excursion capability. In the current review, basic architectural terms first are reviewed and then specific examples relevant to upper extremity anatomy are presented. Specific examples of anatomic considerations required for surgical reconstruction after radial nerve palsy also are detailed. Together, these data show not only the wide variety of architectural designs in human muscles, but the importance of considering architectural design when making surgical decisions.

Advances in upper extremity muscle anatomy have provided surgeons with an understanding of the design of muscles and their suitability for surgical transfer and manipulation. As reported by Kardel,¹⁸ the relationship between structure and function in skeletal muscle has been described and probed for more than a century. A classic study has elucidated the microscopic and ultrastructural properties of skeletal muscle fibers, yielding great insights into their function.⁸ However, less attention

has been given to the excellent and insightful studies of the macroscopic properties of skeletal muscle tissues dating back to the 1600s. This macroscopic arrangement of muscle fibers is known as a muscle's architecture.¹³ Because muscle architecture is the primary determinant of muscle function, understanding this structure and function relationship is of great practical importance, not only to provide a basic understanding of the physiologic basis of force production and movement, but also to provide a scientific rationale for surgery that may involve tendon transfer procedures, to provide guidelines for electrode placement during electromyographic measures of muscle activity, to explain the mechanical basis of muscle injury during normal movements, and to aid in the interpretation of histologic specimens obtained from muscle biopsies. The purpose of the current review is to describe the theoretical significance of muscle architecture and to describe the basic architectural properties of human upper and lower extremity muscles. Some of this information and more advanced topics were presented in another recent review.²⁴

Basic Architectural Definitions

It is well-known that skeletal muscle is highly organized at the microscopic level—witness the incredible number and diversity of electron micrographs and schematics of muscle sarcomeres that have been published in review ar-

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ticles and textbooks.^{7,8} However, with few exceptions, the arrangement of muscle fibers within and between muscles has received much less attention. Muscle fibers often are depicted as projecting in bundles (fascicles) from an origin on a proximal tendon plate to an insertion more distally. This simply does not do justice to the wide array of muscle designs that are apparent throughout the animal kingdom. The architecture of a given muscle is extremely consistent between individuals of the same species giving rise to the concept that certain constraints are present that determine muscle architectural properties.^{5,17,23,25,31,37,39,40,42} Although much attention has been given to factors such as fiber type distribution in determining muscle function, there is no question that function is most strongly determined by a muscle's architecture.⁶

Skeletal muscle architecture is defined as "the arrangement of muscle fibers within a muscle relative to the axis of force generation."²⁰ Although muscle fibers have a relatively consistent fiber diameter between mus-

cles of different sizes and such differences can affect force generation, architectural differences between muscles have much more variability and more strongly affect function. The various types of architectural arrangements are as numerous as the muscles themselves, yet for discussion purposes, the authors describe three general classes of muscle fiber architecture.

Muscles composed of fibers that extend parallel to the muscle's force-generating axis are described as having parallel or longitudinal architecture (Fig 1A). Although the fibers may project along a line parallel to the force-generating axis, experimental studies of mammalian muscle suggest that muscle fibers do not extend the entire muscle length. In fact, detailed studies of muscle fiber lengths show that muscle fibers may not even extend the entire length of a fascicle.^{31,32} Muscles with fibers that are oriented at one angle relative to the force-generating axis are described as having unipennate architecture (Fig 1B). The angle between the fiber and the force-generating

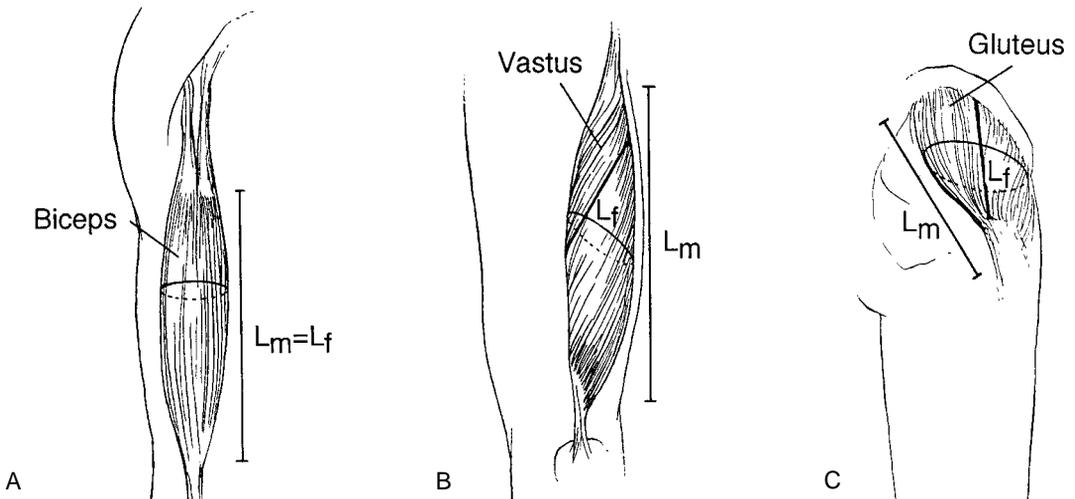


Fig 1A–C. Artist's conception of three general types of skeletal muscle architecture. (A) Longitudinal architecture in which muscle fibers run parallel to the muscle's force generating axis. In this case, the natural example is the biceps brachii. (B) Unipennate architecture in which muscle fibers run at a fixed angle relative to the muscle's force generating axis. Here, the example is the vastus lateralis muscle. (C) Multipennate architecture in which muscle fibers run at several angles relative to the muscle's force generating axis. The example is the gluteus medius muscle. L_m = muscle length; L_f = muscle fibers.

axis has been measured at resting length in mammalian muscles of different designs and varies from approximately 0° to 30° . It becomes obvious to the student performing muscle dissections that most muscles fall into the third and most general category, multipennate muscles which are muscles constructed of fibers that are oriented at several angles relative to the axis of force generation (Fig 1C). Obviously, these three designations are oversimplified, but they do provide a vocabulary with which to describe muscle designs. Because fiber orientation may be unrelated to classic anatomic axes, determination of muscle architecture is impossible from one biopsy or from magnetic resonance imaging (MRI) scans, computed tomography (CT) scans, or ultrasound images, because these methods cannot account for variations in fiber length and orientation that occur along the muscle length. Thus, experimental methods have been developed to characterize the architectural properties of skeletal muscle.¹³

Experimental Determination of Skeletal Muscle Architecture

Quantitative studies of muscle architecture were pioneered by Gans and De Vries¹⁴ who developed precise methodology for defining muscle architecture based on microdissection of whole muscles. Muscles were chemically fixed in 10% buffered formalin to maintain fiber integrity during dissection. Ideally, the muscle would be fixed while attached to the skeleton to preserve its physiologic length, or its physiologic length in the skeleton would at least be observed. After fixation, muscles were dissected from the skeleton, their masses were determined, and their pennation angles (the fiber angle relative to the force-generating axis) and muscle length were measured.

In several studies, the muscles are fixed by direct immersion into fixative, which relies on diffusion of the fixative throughout the tissue thickness to facilitate subsequent dissection.^{5,40} However, for very thick muscles, the quality of the resulting fixation may not be adequate for architectural measurements to be

made. Recently, the authors implemented a high pressure infusion method to chemically fix large human muscles of the shoulder and chest.⁹ Muscles from fresh cadaveric specimens were fixed by high pressure perfusion of 10% buffered formaldehyde via the carotid artery. To achieve adequate pressure, approximately 50-L containers filled with fixative were placed at a height of approximately 3 m above the cadaver. The infusion tubing had a diameter of approximately 5 mm. The carotid artery was cannulated and the fixative was introduced under pressure for approximately 3 days. This method produced the best fixation of muscle tissue from cadaveric specimens that the authors have observed in approximately 10 years of this type of experimentation. Fixation quality was ascertained based on the sharpness and intensity of the lines within the laser diffraction pattern.²⁹ The authors also confirmed, by direct phase contrast microscopy of dissected muscle fibers, that the striation pattern within the sarcomere matrix was excellent using this fixation method.

After fixation, pennation angle (θ) was measured by determining the average angle of the fibers on the superficial muscle surface relative to the muscle's axis of force generation. Of course, this is only an estimate because angles may vary from superficial to deep and even from proximal to distal (Fig 2). Although more sophisticated methods could be developed for measurement of pennation angle, it is doubtful they would provide a great deal more insight into muscle function because variations in pennation angle do not have a great deal of functional importance. Muscle length (L_m) is defined as "the distance from the origin of the most proximal muscle fibers to the insertion of the most distal fibers."²⁰ This is not the same as muscle fiber length (L_f) because of the variable degree of "stagger" seen in muscle fibers as they arise from and insert onto tendon plates. To date, muscle fiber length only can be determined by microdissection of individual fibers from fixed tissues or by laborious identification of fibers on serial sections along the length of the muscle.³²

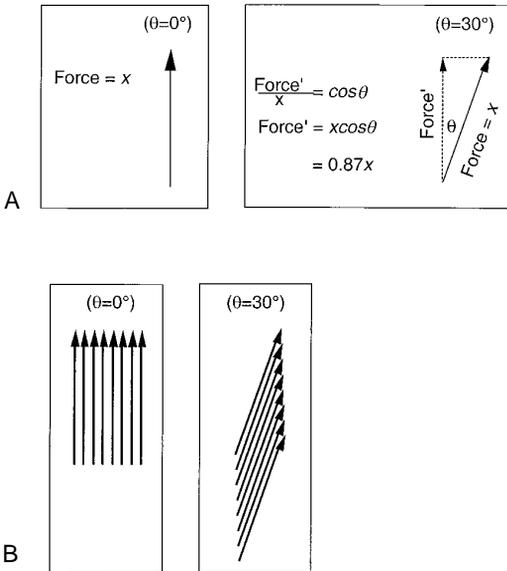


Fig 2A–B. Schematic illustration of the effect of pennation. (A) Muscle fibers oriented parallel to the axis of force generation transmit all of their force to the tendon (left). However, muscle fibers oriented at a 30° angle relative to the force-generating axis transmit only a portion of their force (cosine (30°) = 0.87, or 87%) to the tendon (right). (B) Although only approximately 90% of the muscle fiber force is transmitted to the tendon because of pennation, pennation permits packing of a larger number of fibers into a smaller cross-sectional area.

Unless investigators are explicit when they refer to muscle fiber length, they probably are referring to muscle fiber bundle length because it is extremely difficult to isolate intact fibers, that run from origin to insertion, especially in mammalian tissue.^{31,32} When microdissection is performed, bundles consisting of 10 to 100 fibers may be used to estimate muscle fiber length.

The final experimental step required to perform architectural analysis of a whole muscle is to measure sarcomere length within the isolated fibers. This is necessary to compensate for differences in muscle length that occur during fixation. To conclude that a muscle has long fibers one must ensure that it is truly has long fibers and not that it was fixed in a highly

stretched position. Similarly, muscles with short fibers must be investigated additionally to ensure that they were not fixed at a short sarcomere length. To permit such conclusions, architectural measurements are normalized to a constant sarcomere length that eliminates fiber length variability because of variation in fixation length. This provides a reference value that can be related back to the physiologic length if the relationship between muscle length and joint position is observed. Because sarcomere length also strongly influences muscle force generation, an understanding of the relationship between sarcomere length change and movement has been used in several studies to provide added understanding of muscle design.^{26,27,35,36}

After measurement of the architectural parameters described above, the physiologic cross-sectional area then is calculated. The physiologic cross-sectional area of a muscle is the only architectural parameter that is directly proportional to the maximum tetanic tension generated by the muscle. This value is almost never the actual cross-sectional area of the muscle as measured in any of the traditional anatomic planes, as would be obtained, for example, using a noninvasive imaging method such as MRI, CT scanning, or ultrasound. Theoretically, the physiologic cross-sectional area represents the sum of the cross-sectional areas of all of the muscle fibers within the muscle. It is calculated using Equation 1, which was verified experimentally by Powell et al.³³

$$\text{PCSA (cm}^2\text{)} = \frac{\text{Muscle Mass (g)} \cdot \cos\theta}{\rho \text{ (g/cm}^3\text{)} \cdot \text{Fiber Length (cm)}} \quad \text{(Equation 1)}$$

where PCSA represents physiologic cross-sectional area, ρ represents muscle density (1.056 g/cm³ for mammalian muscle), and θ represents surface pennation angle.

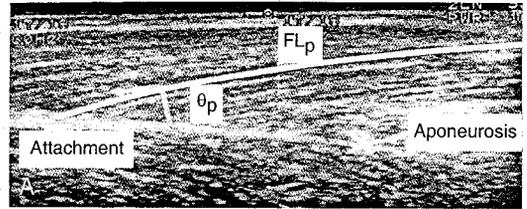
This equation represents muscle volume (mass/density) divided by fiber length and has units of area (in this case, cm²). Because fibers may be oriented at an angle relative to the axis of force generation, the cosine term often is in-

cluded because it is thought that not all of the fiber tensile force is transmitted to the tendons. This idea is shown in Figure 2 where a muscle fiber is shown pulling with \times units of force at an angle θ relative to the muscle axis of force generation. In this configuration, only a component of muscle fiber force actually will be transmitted along the muscle axis, which will be $\times \cos\theta$. Pennation is seen to result in a loss of muscle force relative to a muscle with the same mass and fiber length but without a zero pennation angle.

Does significant fiber rotation occur in muscles from humans? An affirmative answer to this question was provided by Fukunaga and colleagues¹¹ who measured fascicle plane orientation during voluntary contraction of the human quadriceps and dorsiflexor muscles. Their measurements revealed that, during low level voluntary contraction, the vastus lateralis pennation angle increased from 14° with the knee extended to 21° with the knee flexed (Fig 3). During this voluntary contraction, fascicle length decreased tremendously from 126 mm to 67 mm. This provides a real-time picture in which fiber shortening and rotation are simultaneous and normal events of muscle contraction.¹² Fiber rotation during muscle contraction permits tensile force transmission to occur even when muscle fibers are oriented at an angle relative to the muscle's force-generating axis.¹⁹ The fact that pennation angles are small at muscle resting lengths (0° – 30°) probably accounted for the agreement between experiment and theory observed by Powell et al.³³ In predicting muscle force producing capacity, correction for fiber angulation does not seem to be necessary.

Generally, several studies report fascicle lengths rather than fiber lengths.^{3,5,21} However, because fibers apparently terminate end-to-end, functionally, a fascicle seems to perform similar to a muscle fiber of equivalent length.³¹ Fibers may terminate within the muscle belly into the complex extracellular matrix composed of endomysial connective tissue.⁴¹ These connective tissues merge into a final external tendon where force can be applied to bone.

Passive Vastus Lateralis



Active Vastus Lateralis

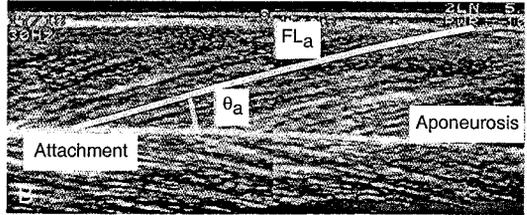


Fig 3A–B. Ultrasound images of human vastus lateralis measured in the sagittal plane with knee at 50° flexion. (A) Muscle image at rest. (B) Muscle image with the quadriceps activated. Muscle activation, even with the knee in a fixed position, results in approximately 7° fiber rotation. Results are even more pronounced as knee angle changes. (Figure adapted from data from Fukunaga T, Ito M, Ichinose Y, et al: Tendinous movement of a human muscle during voluntary contractions determined by real-time ultrasonography. *J Appl Physiol* 8:1430–1433, 1996 and Kawakami Y, Ichinose Y, Fukunaga T: Architecture and functional features of human triceps surae muscles during contraction. *J Appl Physiol* 85:398–404, 1998.)

Architecture of Human Skeletal Muscles

Several architectural investigations have been performed in muscles from the upper and lower limbs of humans.^{3,10,21,23,25} Reported pennation angles usually range from 0° to 30° and the ratio of muscle fiber length to muscle length ranges from approximately 0.2 to approximately 0.6. Even the most longitudinally oriented muscles have fiber bundles that extend only approximately 60% of the muscle length.

Muscles of the Lower Limb in Humans

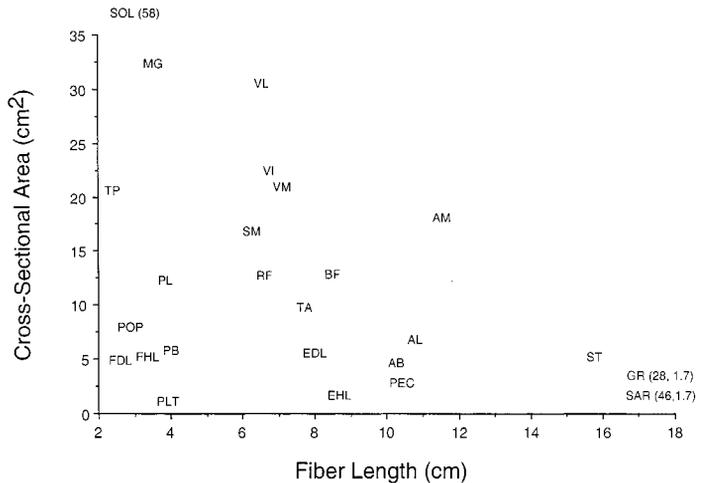
The two most important muscle architectural parameters are muscle physiologic cross-sectional area (proportional to maximum muscle

force) and muscle fiber length (proportional to maximum muscle excursion). These two parameters are shown for human muscles in graphic form (Fig 4) and can be used to make general comparisons among muscle architectural designs. Although each muscle is unique in terms of its architecture, taken as functional groups (hamstrings, quadriceps, dorsiflexors, plantar flexors), numerous generalizations can be made regarding lower extremity muscles. Quadriceps muscles usually are characterized by their relatively high pennation angles, large physiologic cross-sectional areas, and short fibers. In terms of design, these muscles appear suited for the generation of large forces. The hamstrings, however, by virtue of their relatively long fibers and intermediate physiologic cross-sectional areas, seem to be designed for large excursions. Specifically, the sartorius, semitendinosus, and gracilis muscles have extremely long fiber lengths and low physiologic cross-sectional areas, which permit large excursions at low forces (Fig 4). The same appears to be true of the plantar flexors

and dorsiflexors. A general conclusion might be that the antigravity extensors are more designed toward force production, whereas the flexors are more designed for high excursions. The most extreme example of such a design is the soleus muscle, with its high physiologic cross-sectional area and short fiber length, suitable for generating high force with small excursion. This would suit it well for a postural stabilization role.

The relatively high pennation angles of the quadriceps also have implications for muscle biopsy analysis and electromyogram measurement. Because the fibers are relatively short, a biopsy obtained along the length of the muscle may not be representative of all the fibers along the muscle because they are staggered to a high degree. Experimental quantification of repeated biopsy specimens from four rhesus monkeys were studied in three different locations along the length of the soleus, medial gastrocnemius and tibialis anterior muscles.³⁸ The authors reported a much greater fiber type percentage variability between animal sub-

Fig. 4. Scattergraph of the fiber length and cross-sectional areas of muscles in the human lower limb. Fiber length is proportional to muscle excursion, and cross-sectional area is proportional to maximum muscle force. This graph can be used to compare the relative forces and excursions of muscles within the lower limb. AB = adductor brevis; AL = adductor longus; AM = adductor magnus; BF_l = biceps femoris, long head; BF_s = biceps femoris, short head; EDL = extensor digitorum longus; EHL = extensor hallucis longus; FDL = flexor digitorum longus; GR = gracilis; FHL = flexor hal-



lucis longus; LG = lateral gastrocnemius; MG = medial gastrocnemius; PEC = pectineus; PB = peroneus brevis; PL = peroneus longus; PLT = plantaris; POP = popliteus; RF = rectus femoris; SAR = sartorius; SM = semimembranosus; SOL soleus; ST = semitendinosus; TA = tibialis anterior; TP = tibialis posterior; VI = vastus intermedius; VL = vastus lateralis; VM = vastus medialis. (Figure adapted from data from Wickiewicz TL, Roy RR, Powell PL, Edgerton VR: Muscle architecture of the human lower limb. Clin Orthop 179:275–283, 1983.)

jects than between biopsy specimens within a subject. However, they did show that, despite sampling different fibers along muscles with very different architectures (L_f/L_m ratios ranging from 0.23–0.35), it was possible to measure representative percentages within these different muscle regions. Fiber type variability was 5% to 10% within a muscle but as much as 30% between the same muscles of different animal subjects.

Regarding electromyographic measurements, a similar sampling problem may arise as a result of muscle fiber stagger. Electrodes placed in one region of the muscle may not provide an electrical signal that is representative of motor units from different regions of the same muscle.³⁰ This is attributable to two factors, first and most obvious, is the fact that muscle fibers do not extend the length of the muscle and second, there is a natural gradation in fiber type percentage and thus motor unit types from superficial to deep within a muscle. Because motor units are activated in a stereotypical fashion from slow to fast,¹⁶ this may affect duration and amplitude of electromyogram signals measured at different depths. However, the extent to which this inability to sample uniformly affects either clinical judgement or the authors understanding of muscle activation has not been clearly determined.

Muscles of the Upper Limb of Humans

In light of the specialization observed in the lower limb, it probably is not surprising that there also is a high degree of specialization built into upper extremity muscles by virtue of their architecture. For example, the superficial and deep digital flexors are very similar to one another but are different from the digital extensors (Fig 5). As another example, based on its very high physiologic cross-sectional area, the flexor carpi ulnaris is expected to generate very high forces. Examination of this type of information can be used to compare functional properties between muscles that might be transferred surgically to restore lost function. Intuitively, one might consider it important to match the transferred muscle's architectural properties to the architectural properties of the muscle whose function was lost.

Significance of Muscle Architecture in Motor Control

One consequence of the architectural specialization observed throughout the body is that the neuromuscular system is not required to modify muscular force and excursion only by changing nervous input to the muscles. Muscles are intrinsically designed for a specific function; large excursion, for example, and the nervous system merely provide the input sig-

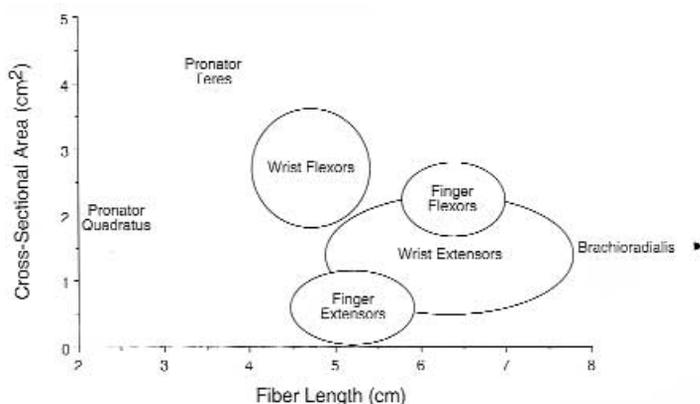


Fig. 5. Scattergraph of the fiber length and cross-sectional areas of muscles in the human forearm. Fiber length is proportional to muscle excursion, and cross-sectional area is proportional to maximum muscle force. This graph can be used to compare the relative forces and excursions of arm and forearm muscles. (Figure adapted from data from Lieber RL, Fazeli BM, Botte MJ: Architecture of selected wrist flexor and extensor muscles. *J Hand Surg* 15A: 244–250, 1990 and Lieber RL,

Jacobson MD, Fazeli BM, Abrams RA, Botte MJ: Architecture of selected muscles of the arm and forearm: Anatomy and implications for tendon transfer. *J Hand Surg* 17A:787–798, 1992.)

nal to modulate the timing and intensity of the activation signal to the muscle. It is as if the nervous system acts as the central control whereas the muscle interprets the control signal into the actual external action by virtue of its intrinsic design.

Significance of Muscle Architecture in Surgical Tendon Transfer

In addition to improving understanding of muscle anatomy and function, elucidation of muscle architecture ultimately may provide information useful for selection of muscles used in tendon transfers. To substitute a lost muscle function, the distal tendons of muscles often are transferred from one position to another.^{2,4,15,34} It would seem reasonable to select a donor muscle with similar architectural properties as the original muscle to match the original muscle's function. Numerous other factors influence donor selection including donor muscle availability, donor muscle morbidity, preoperative strength, integrity, expendability, synergism, transfer route and direction, and surgeon experience and preference.

Surgical Restoration of Digital Extension

The authors envision that architectural differences might be useful in tendon transfer when making a choice involving multiple donors or when a combination of transfers is available for selection. For example, in the surgical restoration of digital extension after high radial nerve palsy described and accepted potential donor muscles that are transferred to the extensor digitorum longus include the flexor carpi radialis, the flexor carpi ulnaris, the flexor digitorum superficialis to the middle finger, and the flexor digitorum superficialis to the ring finger. From the standpoint of architecture alone, the flexor digitorum superficialis to the middle finger most closely resembles the extensor digitorum longus in terms of force generation (cross-sectional area) and excursion (fiber length). This is emphasized by its relatively close position in architectural space of the flexor digitorum superficialis to the middle finger to the extensor digitorum

longus (Fig 5). If one were to compare individual architectural properties, it is clear that the flexor digitorum superficialis to the middle finger has more than enough excursion compared with the extensor digitorum longus whereas the flexor carpi ulnaris has sufficient force-generating potential. If the concern were sufficient force, the flexor carpi ulnaris might be chosen whereas if the concern were excursion, the flexor digitorum superficialis to the middle finger might be chosen. Either way, knowledge of muscle architecture permits an informed decision to be made. Architectural mismatch between the flexor carpi ulnaris and extensor digitorum longus has been blamed for the poor clinical result of this transfer.²⁸

Surgical Restoration of Thumb Extension

To restore thumb extensor function in high radial nerve palsy, potential donors include the flexor digitorum superficialis to the middle finger, the flexor digitorum superficialis to the small finger, and the palmaris longus. Again, in terms of architecture, the flexor digitorum superficialis to the small finger and the palmaris longus are more similar to the extensor pollicis longus, and therefore should provide the force generation and excursion required to restore lost function (Fig 5).

Surgical Restoration of Thumb Flexion

As a final example, after high median nerve palsy, anterior interposes nerve injury, or isolated, irreparable flexor pollicis longus muscle injury, multiple potential donors for transfer to restore thumb flexion are available. These donors include the brachioradialis, the extensor carpi radialis longus, the extensor carpi radialis brevis, the extensor carpi ulnaris, the extensor digiti quinti or the flexor digitorum superficialis to the ring finger. From an architectural standpoint, the extensor carpi radialis brevis, the flexor digitorum superficialis to the ring finger and extensor carpi ulnaris are most similar to the extensor pollicis longus (Fig 5). A simple quantitative method for comparing architectural properties between muscles has been reported.²²

Mechanical Properties of Muscles With Different Architectures

As stated above, muscle force is proportional to physiologic cross-sectional area whereas muscle velocity is proportional to fiber length. By stating that velocity is proportional to fiber length, it is implicit that the total excursion (active range) of a muscle also is proportional to fiber length.

Comparison of Two Muscles With Different Physiologic Cross-Sectional Areas

Suppose that two muscles had identical fiber lengths and pennation angles, but one muscle had twice the mass (equivalent to one muscle having twice the number of fibers and twice the physiologic cross-sectional area). The functional difference between these two muscles is shown in Figure 6. The muscle with twice the physiologic cross-sectional area has a length-tension curve with the same shape but is amplified upward by a factor of two. Thus, the maximum tetanic tension (P_0) of the larger muscle will be twice that of the smaller muscle. Similarly, comparison of schematic force-velocity curves indicates that the differences between muscles simply will be an upward shift in the maximum tetanic tension for the larger muscle, but the curve retains the same shape. If both curves were plotted on relative scales (percent maximum tension instead of absolute tension), the two muscles would appear to have identical properties. This shows that although architectural properties profoundly affect the extrinsic muscle properties (the properties that vary with absolute muscle size, such as the maximum tetanic tension, physiologic cross-sectional area or mass), they have no effect on its intrinsic properties (the properties that are independent of absolute muscle size, such as the shape of the length-tension or force-velocity curves, or fiber length-to-muscle length ratio).

Comparison of Two Muscles With Different Fiber Lengths

Considering functional differences between two muscles with identical physiologic cross-

sectional areas and pennation angles but different fiber lengths, the schematic in Figure 7 shows that the effect is to increase muscle velocity (or muscle excursion). Peak absolute force of the length-tension curves is identical between muscles, but the absolute muscle active range is different. For the same reason that fiber length increases the active muscle range of the length-tension relationship, it causes an increase in the muscle's absolute maximum

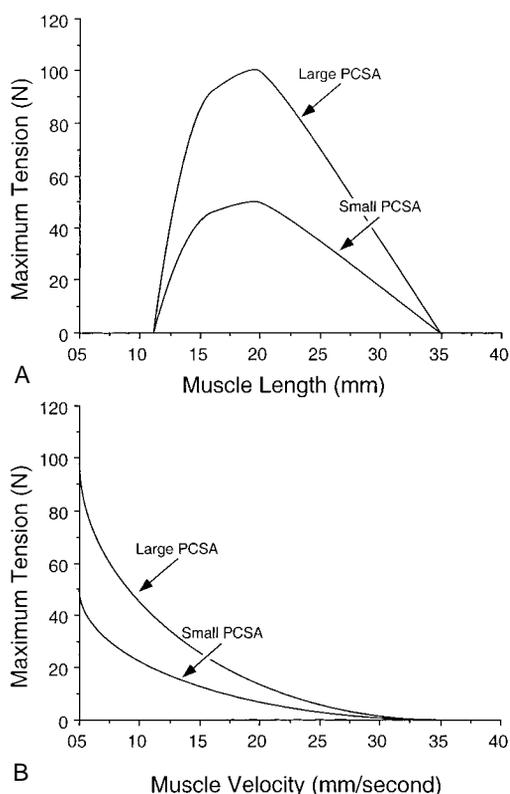


Fig 6A–B. Schematic drawing of two muscles with different physiologic cross-sectional areas but identical mass. (A) Comparison of isometric length-tension properties. (B) Comparison of isotonic force-velocity properties. The effect of increased physiologic cross-sectional area with identical fiber length is to shift the absolute length-tension and force-velocity curves to higher values, but with retention of the same range and intrinsic shape. PCSA = physiologic cross-sectional area.

contraction velocity (V_{max}). As in the example with altered physiologic cross-sectional area, fiber length increases these absolute properties but has no effect on the intrinsic properties of the muscle. Experimental support for this concept was obtained indirectly in a study on the cat semitendinosus muscle.¹ When only the proximal head was activated, its maximum contraction velocity was 224 mm per second whereas when only the distal head was activated, its maximum contraction velocity was 424 mm per second. Then, when both heads

were activated simultaneously, the whole muscle maximum contraction velocity was 624 mm per second, or the sum of the two velocities. These data indicate that the longer the fibers in series (equivalent of saying the greater number of sarcomeres in series), the greater the muscle contraction velocity. As expected, maximum isometric tension essentially was the same regardless of which activation pattern was used.

Range of Motion as a Function of Architecture

Muscles with longer fibers have a longer functional ranges than muscles with shorter fibers. Does this necessarily indicate that muscles with longer fibers are associated with joints that have larger ranges of motion? No. It is true that a muscle with longer fibers does have a longer working range but the amount of muscle fiber length change that occurs as a joint rotates depends on the muscle moment arm, the mechanical advantage that a muscle has at a particular joint. This idea is shown in Figure 8, where a simulated muscle is attached to a joint using two different moment arms. In Figure 8A, the moment arm is much greater than the moment arm shown in Figure 8B. This means that in Figure 8A, the muscle fibers will change length much more for a given change in joint angle compared with the same change in joint angle in Figure 8B. As a result, the active range of motion (ROM) for the muscle-joint system shown in Figure 8A will be much smaller (30°) compared with that shown in Figure 8A (70°) despite that their muscular properties are identical. Therefore, the design of a muscle when considered in isolation may or may not be directly related to the actual function of a muscle once placed in the skeletal system.

It now is important to qualify the previous statement about muscle design and architecture. Muscles that are designed for speed based on their long fibers actually may not produce large velocities if they are placed in the skeleton with a very large moment arm. The increased moment arm results in a very

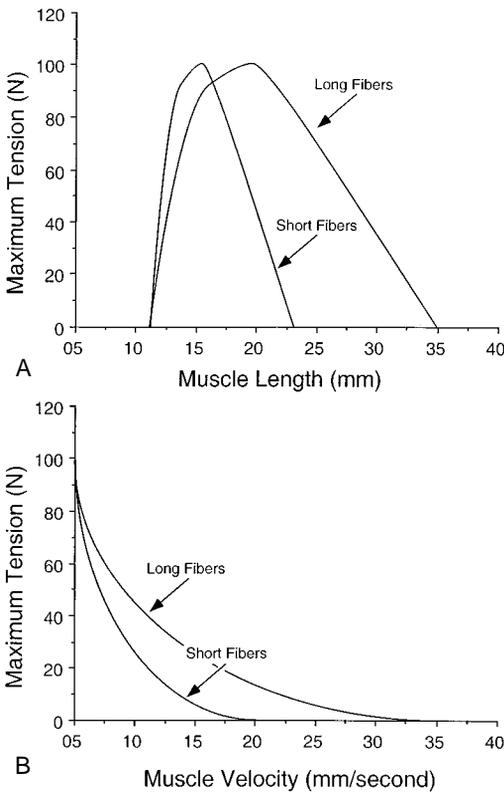


Fig 7A-B. Schematic drawing of two muscles with different fiber lengths but identical physiologic cross-sectional areas. (A) Comparison of isometric length-tension properties is shown. (B) Comparison of isotonic force-velocity properties is shown. The effect of increased fiber length is to increase the absolute range of the length-tension curve and absolute velocity of the force-velocity curve, but with retention of the same peak force and intrinsic shape.

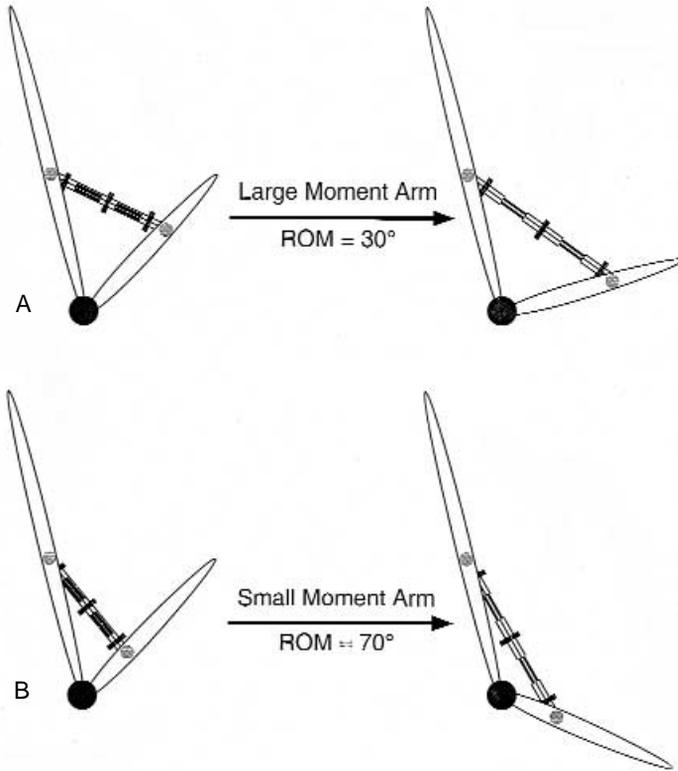


Fig 8A–B. Schematic illustration of muscle active range of motion (ROM) changing attributable to altered muscle moment arm. (A) Schematic muscle attached to joint with a large moment arm results in only 30° range of motion because sarcomere length change with joint rotation is fairly large. (B) Schematic muscle attached to joint with a small moment arm results in 70° range of motion because sarcomere length change with joint rotation is relatively small. (Adapted with permission from Lieber RL: *Skeletal Muscle Structure and Function. Implications for Physical Therapy and Sports Medicine*. Baltimore, Williams & Wilkins 1992.)

large joint moment so that the muscle would be highly suited for torque production but at low angular velocities. Similarly, a muscle that is designed for force production because of the large physiologic cross-sectional area, if placed in position with a very small moment arm, actually may produce high joint excursions or angular velocities.

Skeletal muscle architecture is the structural property of whole muscles that dominates their function. The fact that different muscles contain such different and reproducible architectural designs suggests that architecture is under tight control of the muscle fibers. Future physiologic studies will provide insights into the rationale for muscles in which the stereotypical functions are not clear. In addition, basic science studies of muscle structural and functional proteins will provide insights into the cellular regulation of serial sarcomere number, which could have significant implications in the case of surgical trans-

fer of muscles. Several questions remain unanswered such as: What is the nature and extent of muscle adaptation that occurs after surgery? Do all muscles adapt to the same extent? Does muscle architecture accurately predict intraoperative behavior of muscle? Can adaptation be facilitated by such means as intraoperative transfection, electrical stimulation, regeneration, or manual manipulation? Future studies should provide insights into these questions and enable surgeons to more effectively treat the various musculoskeletal disorders encountered.

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