Skeletal Muscle Architecture: Implications for Muscle Function and Surgical Tendon Transfer

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ABSTRACT: Skeletal muscles have mechanical properties that are well-described by the length-tension relationship (for isometric contractions) and the force-velocity relationship (for isotonic contractions). These two intrinsic properties are scaled for a given muscle based on its architectural properties. Muscle active force-generating range is determined by muscle fiber length, while maximum muscle force is determined by physiologic cross-sectional area. These and other architectural properties should be matched between muscles when planning surgical tendon transfers in order to closely match donor and recipient muscles. Finally, the fiber length/moment arm ratio of a muscle-joint combination must be considered when describing strength because strength is a manifestation of both muscle and joint properties and not either alone. Unfortunately, detailed description of normal musculoskeletal design or optimal transfer strategy cannot be made until more basic science studies of the musculoskeletal system are conducted.

During their training, therapists and physicians usually take several courses that include skeletal muscle anatomy and physiology. It is interesting to note that almost all therapists and physicians learn the major portions of the muscle sarcomere (the A-band, Z-band, etc.) and can describe cross-bridge action within the sarcomere. However, few can describe skeletal muscle architecture, which is much more applicable to human performance, rehabilitation, and surgical outcome. This special emphasis results from the fact that the majority of physiology textbooks present skeletal muscle contraction from a cellular point of view. This is simply because the majority of our knowledge of skeletal muscle contraction is at the cellular level. Only recently have the architectural differences between whole muscles been investigated and quantified. These studies suggest a number of new ideas: (1) skeletal muscle architecture is the most profound determinant of whole muscle function and (2) muscles are composed of different fiber types, which reflect the developmental process and level of muscle use. The purpose of this review is to provide the therapist with a description of basic muscle function, muscle architecture, its functional consequences, and its applicability to surgical procedures involving skeletal muscles. Much of this information is digested from recent articles in Journal of Hand Surgery and a recently published textbook on applied skeletal muscle physiology.

To understand the functional consequences of muscle architecture, it is first necessary for us to review two fundamental mechanical properties of skeletal muscle: the length-tension relationship and the force-velocity relationship.

LENGTH-TENSION RELATIONSHIP: ISOMETRIC MUSCLE CONTRACTION

The isometric length-tension curve is generated by maximally stimulating a skeletal muscle at a series of discrete lengths and measuring the tension generated by the muscle at each length. When maximum tetanic tension at each length is plotted against length, a relationship such as that shown in Figure 1 is obtained. While a general description of this relationship was established early in the history of biologic science, the precise structural basis for the length-tension relationship in skeletal muscle was not elucidated until the sophisticated mechanical experiments of the early 1960s were performed. These experiments defined the precise relationship between myofilament overlap and tension generation, which we refer to today as the sarcomere length-tension relationship. In its most basic form, the length-tension relationship means that isometric tension generation in skeletal muscle is a direct function of the magnitude of overlap between actin and myosin filaments. Thus, when a muscle length is either very long or very short, low isometric force is generated. However, at an "optimal" length (where maximum interaction between myosin and actin filaments occurs), muscle generates its maximal force.

FORCE-VELOCITY RELATIONSHIP: ISOTONIC MUSCLE CONTRACTION

Unlike the length-tension relationship, the force-velocity relationship does not have a precisely iden-
FIGURE 1. The sarcomere length—tension curve for frog skeletal muscle obtained using sequential isometric contractions in single muscle fibers. Insets show schematic arrangement of myofilaments in different regions of the length—tension curve. Dotted line represents passive muscle tension. Tension is expressed relative to an arbitrary maximum.

FIGURE 2. The muscle force—velocity curve for skeletal muscle obtained using sequential isotonic contractions in single fibers. Insets show schematic representation of cross-bridges. Note that force increases dramatically upon forced muscle lengthening. Force (tension) and velocity are expressed on relative scales.

tifiable anatomic basis. The force—velocity relationship means that the force generated by a muscle is a function of its velocity. It can also be stated in the reverse—that contraction velocity depends on the force resisting the muscle. Historically, the force—velocity relationship was used to define the dynamic properties of the cross-bridges that cycle during muscle contraction.

The force—velocity relationship, like the length—tension relationship, is a curve that actually represents the results of many experiments plotted on the same graph. Experimentally, a muscle is maximally stimulated and allowed to shorten (or lengthen) against a constant load. The muscle velocity during shortening (or lengthening) is measured and then plotted against the resistive force. The general form of this relationship is shown in Figure 2. On the horizontal axis is plotted muscle velocity relative to maximum velocity ($V_{max}$), while on the vertical axis is plotted muscle force relative to maximum isometric force ($P_i$).

Concentric Contractions—Muscle Actively Shortening

When a muscle is activated and required to lift a load that is less than its maximum isometric tension, the muscle begins to shorten. Contractions involving muscle shortening are known as concentric contractions. In concentric contractions, the force generated by the muscle is always less than the muscle’s maximum isometric tension ($P_i$). As the load the muscle must lift decreases, contraction velocity increases. This occurs until the muscle finally reaches its maximum contraction velocity, $V_{max}$. $V_{max}$ is a parameter used to define a muscle’s dynamic properties, and is related to both fiber type distribution and muscle architecture. It is important to note that the force—velocity relationship is a steep rectangular hyperbola. In other words, force drops off rapidly as velocity increases. For example, if a muscle shortens at only 1% of its maximum contraction velocity (ex-
tremely slow), tension drops by 5% relative maximum isometric tension. Similarly, as contraction velocity increases to only 10% maximum (easily attainable physiologically), muscle force drops by 35%! Note that even when muscle force is only 50% maximum, muscle velocity is only 17% \( V_{\text{max}} \). The take-home lesson is that as a muscle is allowed to shorten, force drops precipitously.

Eccentric Contractions—Muscle Actively Lengthening

As the load on a muscle increases, it reaches a point where the external load is greater than the load the muscle can generate (negative velocities in Fig. 2). The muscle is activated, but it is forced to lengthen due to the high external load. This is referred to as an eccentric contraction ("contraction" in this context does not necessarily indicate shortening!). There are two main features that characterize eccentric contractions. First, the absolute tensions are very high relative to the muscle's maximum tetanic tension-generating capacity. Second, the absolute tension is relatively independent of lengthening velocity. This suggests that skeletal muscles are very resistant to lengthening, a property that comes in handy for many normal movement patterns.

As a side note, eccentric contractions are currently a "hot" area of research for at least three reasons: First, much of a muscle's normal activity occurs while it is actively lengthening, so that eccentric contractions are physiologically common. Second, muscle injury and soreness are selectively associated with eccentric contraction. Finally, muscle strengthening is greatest using exercises that involve eccentric contractions.

SKELETAL MUSCLE ARCHITECTURE

Skeletal muscle is not only highly organized to function at the microscopic level, the arrangement of the muscle fibers at the macroscopic level also demonstrates a striking degree of organization. In making comparisons between various muscles, certain factors such as fiber type distribution are important, but there is no question that an important factor in determining a muscle's contractile properties is the muscle's architecture.

Skeletal muscle architecture is defined as "the arrangement of muscle fibers relative to the axis of force generation." While muscle fibers have a relatively consistent fiber diameter between muscles of different sizes, the arrangements of these fibers can be quite different. The various types of arrangement are as numerous as the muscles themselves, but for convenience we often refer to three types of fiber architecture.

Examples of Muscle Architecture

Muscles with fibers that extend parallel to the muscle force-generating axis are termed parallel or

FIGURE 3. Generalized picture of muscle architectural types. Skeletal muscle fibers may be oriented along the muscle's force-generating axis (A), at a fixed angle relative to the force-generating axis (B), or at multiple angles relative to the force-generating axis (C). Each of these represents an idealized view of muscle architecture and probably does not adequately describe any single muscle. ML = muscle length; FL = fiber length.

longitudinally arranged muscles (Fig. 3A). While the fibers extend parallel to the force-generating axis, they never extend the entire muscle length. Muscles with fibers that are oriented at a single angle relative to the force-generating axis are termed unipennate muscles (Fig. 3B). The angle between the fiber and the force-generating axis generally varies from 0° to 30°. It is obvious when preparing muscle dissections that most muscles fall into the final and most general category, multipennate muscles—muscles composed of fibers that are oriented at several angles relative to the axis of force generation (Fig. 3C). As discussed below, an understanding of muscle architecture is critical to understanding the functional properties of different-sized muscles.

Effect of Muscle Architecture on Muscle Function

The functional effect of muscle architecture can be simply stated as: muscle force is proportional to physiological cross-sectional area (PCSA), and muscle velocity is proportional to muscle fiber length. In stating that velocity is proportional to fiber length, it is implicit that the total excursion (active range) of a muscle is also proportional to fiber length. Thus, increasing fiber length results in both increased muscle velocity and increased excursion. It is probably apparent, based on the brief discussion of architecture above, that neither fiber length nor PCSA can easily be deduced based on gross muscle inspection. Detailed dissections of cadaveric muscles are required for architectural determination. However, after determining architectural properties, it is possible to understand how much force the muscle generates and how fast it contracts (or how far it contracts). Following are

*Reference 21 provides a description of the methodology.
two specific architectural examples and their impact on the length--tension and force--velocity relationships.

Comparison of two muscles with different PCSAs. Suppose that two muscles had identical fiber lengths and penning angles, but one muscle had twice the mass (equivalent to saying that one muscle had twice the number of fibers and thus twice the PCSA). What would be the difference in their mechanical properties? How would the length--tension and force--velocity curves be affected?

The schematic in Figure 4 demonstrates that the only effect is to increase maximum tetanic tension so that the length--tension curve has the same basic shape but is simply amplified upward in the case of the stronger muscle. Similarly, the force--velocity curve simply changes the location of P_0, but the curve retains the same basic shape. Note that if both curves are plotted on relative scales (i.e., percentage of maximum tension instead of absolute tension), the two muscles of different architectures appear to have identical properties. This demonstrates that while architectural properties profoundly affect the muscle's extrinsic properties (i.e., the properties that vary with absolute muscle size, such as PCSA or mass), they have no effect on its intrinsic properties (i.e., the properties that are independent of absolute muscle size, such as fiber length/muscle length ratio).

![Figure 4](image1.png)

**Figure 4.** Schematic length--tension (A) and force--velocity (B) curves for muscles with different cross-sectional areas but identical fiber lengths.

![Figure 5](image2.png)

**Figure 5.** Schematic length--tension (A) and force--velocity (B) curves for muscles with identical cross-sectional areas but different fiber lengths. PCSA = physiologic cross-sectional area.

Comparison of two muscles with different fiber lengths. Let us consider the effects of architecture using an example of two muscles with identical PCSAs and penning angles but different fiber lengths. As shown in Figure 5, the effect is to increase the muscle velocity (or, stated identically, to increase the muscle excursion). The peak absolute forces of the length--tension curves are identical, but the absolute muscle active ranges are different. That sounds a lot like active range of motion (ROM), a measurement that is extremely important in clinical evaluation. In fact, it is directly related to ROM—ROM is a direct result of muscle architecture and the joint properties on which the muscle acts.

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 contraction velocity (V_max). Again, while the fiber length increase causes an increase in these extrinsic properties, it has no effect on the intrinsic properties of the muscle. A similar exercise can be performed comparing muscles with different PCSAs and fiber lengths.

We are now in a position to characterize, in a highly descriptive manner, the various muscles of the upper extremity. Based on the information provided above, it is clear that the two most important
structural parameters in muscles are its fiber length and its PCSA. Do these parameters vary between muscles in the upper extremity? Is there a rationale for the various architectural features observed?

Architectural Studies of the Human Arm Muscle

The pioneering studies of upper extremity muscle architecture were performed by the renowned hand surgeon Paul Brand. However, recently, more sophisticated experimental studies of upper extremity muscle architecture have been performed in Rochester, Los Angeles, and San Diego. The take-home lesson from all of these studies is the same: skeletal muscles demonstrate a remarkable degree of architectural specialization. This specialization appears to be well-suited to each muscle in order that it might perform its task. Since the two most important architectural parameters are fiber length and PCSA, these have been plotted on a scatter graph in Figure 6 for rapid appraisal. Since fiber length is proportional to excursion and PCSA is proportional to muscle force, these graphs can be used to understand the functional specializations of each muscle.

As an example, let us compare the pronator teres (PT) with the brachioradialis (BR). The two muscles have approximately the same mass. Clearly, the architectural features are almost at opposite ends of the spectrum (note the wide separation in Fig. 6). The BR, with its long fibers (121 mm) arranged at a small pennation angle (2.4°), has a PCSA (1.3 cm²) that is only one-third that of the PT (4.1 cm²), with its short fibers (36.4 mm) that are more highly pennated (9.6°).

Calculation of an Architectural “Difference Index”

Many parameters can be measured from each muscle. However, to simplify comparisons between muscles in terms of their architecture, we defined the “difference index,” $\delta_{2-1}$, between muscles 1 and 2, based upon the five “most different” parameters: fiber length (FL), PCSA, muscle length (ML), FL/ML ratio, and mass. This index can be viewed as a modification of the well-known algebraic distance formula used to calculate the distance between two points in a plane. Recall that the distance between points with the coordinates $(x_1, y_1)$ and $(x_2, y_2)$ is given as:

$$\text{distance} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

In the same manner, the “difference” between two muscles in “architectural space” can be represented as the difference index:

$$\delta_{2-1} = \sqrt{(FL_2 - FL_1)^2 + (PCSA_2 - PCSA_2)^2 + (FL/ML_2 - FL/ML_1)^2 + (ML_2 - ML_1)^2 + (mass_2 - mass_1)^2}$$

where FL₂ to mass₁ represent the raw architectural data from muscles 2 and 1, respectively. Raw data are first appropriately weighted to participate equally in the index. Using this system, high numbers (e.g., $\delta > 0.8$) suggest muscles that are architecturally different, while low numbers (e.g., $\delta < 0.3$) represent muscle pairs that are architecturally similar. These values were calculated for all possible muscle pairs and can be used to make surgical decisions regarding replacement of one muscle with another. Obviously, muscle pairs that are relatively “close” together in

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Refer to Table 3 of reference 17 for the values.
Figure 6 have relatively small difference indices because fiber length and muscle length play heavily in the calculation of $\delta_{2-1}$.

Implications for Tendon Transfer

In addition to improving our understanding of muscle anatomy and function, elucidation of muscle architecture may ultimately provide information useful for selection of muscles used in tendon transfers. To substitute a lost muscle function, it would seem reasonable to select a donor muscle with architectural properties similar to those of the original muscle. (Of course, numerous other factors influence donor selection, including donor muscle availability, morbidity, preoperative strength, integrity, expendability, synergism, transfer route, and direction, and surgeon experience and preference.)

Surgical restoration of digital extension. We envision that the difference index 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 following high radial nerve palsy (Fig. 7A), described and accepted potential donor muscles (which are transferred to the extensor digitorum communis (EDC)) include the flexor carpi radialis (FCR) as described by Brand, the flexor carpi ulnaris (FCU) as described by Jones, Goldner, and Riordan, the flexor digitorum superficialis (FDS) to the middle finger (M) as described by Boyes, and the FDS to the right finger as described by Beasley. From the standpoint of architecture alone, the FDS (M) most closely resembles the EDC in terms of force generation (i.e., cross-sectional area) and excursion (i.e., fiber length). This is emphasized by its relatively low difference index of 0.41 (compared with the FCU difference index of 0.76; Fig. 7A). If one were to compare individual architectural properties, it is clear that the FDS (M) has more than enough excursion compared with the EDC, while the FCU has sufficient force-generating potential. Thus, if the concern were sufficient force, the FCU might be chosen, while if the concern were excursion, the FDS (M) might be chosen. Either way, a knowledge of muscle architecture permits the informed decision to be made.

Surgical restoration of thumb extension. To restore extensor pollicis longus (EPL) function in high radial nerve palsy, potential donors include the FDS to the middle finger as described by Goldner, the FDS to the small finger as described by Beasley, and the PL as described by Brand and Riordan. Again, in terms of architecture, the FDS to the small finger and the PL are more similar to the EPL, with difference indices of only 0.19 and 0.35, respectively, and therefore should provide the force generation and excursion required to restore lost function (Fig. 7B).

Surgical restoration of thumb flexion. As a final example, following high median nerve palsy, anterior interosseous nerve injury, or isolated, irreparable flexor pollicis longus (FPL) muscle injury, multiple potential donors for transfer to restore thumb flexion are available. These donors include the BR as described by Burkhalter, Goldner, and Smith and Hastings, the extensor carpi radialis longus (ECRL) as described by Boyes and Brand, the extensor carpi radialis brevis (ECRB) as described by Boyes, the extensor carpi ulnaris (ECU) as described by Brand and Riordan, the extensor digiti quinti (EDQ) as described by Littler, and the FDS to the ring finger (R). From an architectural standpoint, the ECRB, the FDS (R) and the ECU are most similar to the FPL, with difference indices of only 0.44, 0.32, and 0.30, respectively (Fig. 7C).

To review, although the importance of architecture has been emphasized by Brand et al. and Smith and Hastings, often little attention has been given to this fundamental muscle property. However, when one considers the profound influence of architecture on muscle function, it would seem that architecture deserves further emphasis to provide additional information that may be relevant to extremity function and restoration.

Fiber Length/Moment Arm Considerations in Tendon Transfer

The above discussion has been concerned with describing muscular properties and matching the properties of a donor muscle to those of a recipient muscle. However, this must be viewed as an oversimplification because muscle force is always expressed externally as a joint torque—the product of muscle force and moment arm. For any muscle–joint system, we must define both the muscle force-generating properties (determined primarily by architecture, as described above) and joint kinematics (the "mechanical advantage" of the muscle as a function of joint angle). Unfortunately, the detailed relationship between human muscle and joint properties has not been thoroughly studied. To clearly understand the stated problem, refer to Figure 8. The top portion of the figure shows hypothetical length–tension relationship, expressed as a tension–joint angle relationship. For the purpose of this discussion, assume

**Figure 8.** Conceptual question posed by the relative angular location of the angle at which maximum muscle force occurs and the angle corresponding to maximum moment arm. A, muscle force as a function of joint angle. B, moment arm as a function of joint angle. Small vertical lines represent peaks of each curve. Horizontal arrows emphasize that relative angular relationship between these curvess is generally unknown. Force and moment arm are expressed on relative scales.
that a muscle increases force and then decreases as a trigonometric sine function as a joint rotates (Fig. 8A). Note that the detailed form of both muscle and moment arm curves is relatively arbitrary and only intended to illustrate muscle–joint interaction. Figure 8B depicts a typical moment arm curve. Since we established that the moment is simply the product of muscle force and moment arm, the joint moment results from the product of these two curves. However, the key question that must be addressed is, what is the relative angular relationship between the muscle and joint properties (arrows in Fig. 8)? That is, is muscle force maximum at the same angle where moment arm is maximum? If not, at what joint angle is muscle force maximum? If the two curves are offset relative to one another (vertical dotted lines), their product will be dramatically altered. In fact, such an alteration can easily occur as a result of surgical tendon transfer.

Thus, understanding the relationship between muscle and joint properties is important from the point of view of understanding the normal design of the musculoskeletal system. It is also important in providing a scientific basis for surgical procedures that involve movement or transfer of muscles from one position to another. If we are to mimic the natural function of the musculoskeletal system, we must understand the relationship between muscles and joints. Specifically, we must define the relative angular relationship between the two curves in Figure 8.

For example, suppose a muscle–joint system were configured such that, by extending from 40° to 80°, the muscle went from its minimum to its maximum length (Fig. 9A). Now, suppose the muscle fiber length were significantly increased. What happens to joint ROM? Clearly, since more sarcomeres are in series to take up the length change, joint ROM increases. Now the muscle can extend from 70° to 145°—a total of 75° (compared with the previous 40°; Fig. 9B). Therefore, by increasing fiber length, active ROM has increased from 40° to 75°! This demonstrates the intimate interaction between the muscle and the joint about which it rotates. If this change in fiber length resulted from tendon transfer, the joint strength and active ROM would also be altered.

Based on this example, we can see that the ratio between muscle fiber length (number of sarcomeres in series) and moment arm will influence the amount of sarcomere shortening that will occur during joint rotation. This ratio can be calculated for any muscle joint system as:

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\text{ratio} = \frac{\text{fiber length}}{\text{moment arm}}
\]

and will determine the relative influence of the muscle on the muscle–joint torque generator.24 As we have seen, if fiber length is very long compared with moment arm, relatively little sarcomere length change will occur during joint rotation, and muscle force

![FIGURE 9. Schematic illustration of muscle active range of motion changing due to altered muscle fiber length. A, Short muscle fibers result in only 40° range of motion. B, Long muscle fibers result in a range of motion of about 75°.](image-url)
change will contribute little to the joint moment. If, however, fiber length is very short and moment arm is long, the sarcomeres will change length a great deal during joint rotation, and so will muscle force. This dramatically affects the muscle contribution to the joint moment.

CONCLUSION

Detailed description of normal musculoskeletal design or optimal transfer strategy cannot be made until more basic science studies of the musculoskeletal system are conducted. Based on these types of studies, our understanding of normal function will be improved and rational bases can be developed for the various rehabilitative and surgical procedures performed.

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