The Effects of Strength Training on Muscle Architecture in Humans

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The present paper reviews previous studies on changes in muscle architecture in humans as a result of strength training. Muscle architecture here refers to 1) muscle size, 2) pennation angle, and 3) muscle fiber length. Training-induced changes are summarized respectively.

A typical outcome of strength training is muscle hypertrophy, which is manifested as an increase in muscle size evaluated by cross-sectional area and muscle volume. However, changes also occur in pennation angles and, possibly, in muscle fiber lengths. Increased pennation angles after training have the detrimental effect of producing a reduced force transmission from muscle fibers to tendon, which might lead to a decrease in specific tension or muscle force per physiological cross-sectional area. Recent in vivo studies on human muscles have revealed that changes in pennation angles resulting from training and contraction are much greater than previously thought.

Keywords: muscle cross-sectional area, pennation angle, fiber length, specific tension

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2. Training-induced changes in muscle architecture

2.1. Muscle size

As a result of strength training, there occurs an enlargement of muscle fibers and, hence, an increase in muscle size (MacDougall, et al., 1980). In human studies, muscle size is assessed from partial information such as the thickness of the muscle belly or CSA of a muscle or muscle groups. Although there is a highly significant correlation \((r = 0.9)\) between the thickness and CSA of a muscle (Martinson and Stokes, 1991), the latter is frequently used in training studies, since the former is only a partial, one-dimensional measure of muscle. To measure muscle CSA in humans, imaging techniques such as ultrasonography (US, Dons, et al., 1979; Ikai and Fukunaga, 1970; Ichinose, et al., 1998), computed tomography (CT, Alway, et al., 1990; Davies, et al., 1988; Jones and Rutherford, 1987; Luthi, et al., 1986), and magnetic resonance imaging have been used (MRI, Akima, et al., 2003; Cureton, et al., 1992; Housh, et al., 1992; Kawakami, et al., 1995). It has been shown in these studies that muscle CSA increases by 5 – 20% as a result of strength training lasting 5 – 12 weeks.

In reality, muscle presents three-dimensionally, and a training-induced enlargement takes place throughout the muscle. Therefore, it is more appropriate to evaluate muscle size over the entire muscle belly. Recently, taking CSAs serially from the proximal to the distal end of the muscle has been possible by MRI. This method was initially introduced by Mungiole and Martin (1990), and later developed by Fukunaga, et al., (1992). It was shown by this method that muscle CSA increases by 5 – 20% as a result of strength training lasting 5 – 12 weeks.

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2.2. Pennation angle

Skeletal muscles are roughly divided into two types with respect to the arrangement of fascicles or muscle fibers, i.e., parallel-fibered muscles in which fibers with length close to that of the whole muscle lie almost parallel to the muscle line of action, and pennate muscles, in which short fibers insert into tendons at an angle to the muscle line of action (Gans and de Free 1987). The angulation of muscle fibers relative to the line of action of muscle in pennate muscles is known as pennation angle.

Fiber pennation is considered to be a packing strategy by which more fibers can be contained in a muscle compared with parallel-fibered muscles (Gans and Gaunt, 1991). The gastrocnemius, a typical unipennate muscle, has more than 1 million fibers while the parallel sartorius muscle has approximately 100,000 fibers (McComas, 1996). Thus, the physiological CSA (total CSAs of fibers in a muscle) of pennate muscles is larger than parallel-fibered muscles (Yamaguchi, et al., 1990). From this fact, it has been thought that pennate muscles are designed for force production while parallel-fibered muscles are designed for excursion and speed (Huijing and Woittiez, 1984; Lieber and Blevins, 1989). Recently, however, pennate muscles have been shown to possess prominent power (force x speed) potential owing to muscle-tendon interaction (Kawakami, et al., 2002).

Kawakami, et al. (1993, 2000a) measured pennation angles of the triceps brachii muscle in vivo using ultrasonography for subjects including normal individuals and highly-trained bodybuilders. The pennation angles were within the range of 5° and 55°, which were smaller and much greater than the conclusion has yet made regarding the intra-muscle inhomogeneity of muscle hypertrophy. However, it has been shown that muscle volume is related more to joint torque than to CSA (Fukunaga, et al., 2001). Thus, when evaluating joint performance from muscle size, the muscle volume rather than CSA should be measured. Recent studies have adopted muscle volume as a measure of muscle size (e.g., Kanehisa, et al., 2002; Tracy, et al., 1999; Tesch, et al., 2003); however, other studies exist that evaluate muscle size from a single, anatomical CSA (e.g., Ahtiainen, et al., 2005; Gondin, et al., 2005; Hubal, et al., 2005).
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published data on human cadavers (Yamaguchi, et al., 1990). They further investigated the relationship between pennation angles and muscle thickness, and found a significant correlation (Figure 2), which provided experimental evidence of the contention in previous studies that muscle hypertrophy accompanies an increase in pennation angles (Jones and Rutherford, 1987; Maxwell, et al., 1974; Narici, et al., 1989). It was further confirmed, through a longitudinal study, that hypertrophy by strength training was actually accompanied by an average increase in pennation angles in the triceps brachii muscles that increased their total volume by 32% and physiological CSA by 33% (Kawakami, et al., 1995). Henriksson-Larsen, et al., (1992) failed to find a significant correlation between pennation angles and muscle fiber CSA in the human vastus lateralis muscle. Rutherford and Jones (1992) found a correlation between pennation angles and muscle CSA of the vastus lateralis; however, they reported no changes in pennation angles after strength training that induced an increase in muscle CSA by 5%. These studies suggest inter-muscle differences in training-induced responses in fiber architecture. However, later Aagaard, et al., (2001) found both a correlation between pennation angles and muscle volume and an increase in pennation angle after a strength training of the vastus lateralis muscle that increased muscle CSA and volume by 10%. It appears, therefore, that the differences in the tendency between the studies are simply due to the magnitude of the muscle hypertrophy resulting from training, and that the increase in pennation angles is a general outcome of hypertrophied pennate muscles.
(Figure 3) (Kawakami, et al., 2002). This change appears to be independent of gender difference (Ichinose, et al., 1998). Clearly, such a change might cause a different time-course of changes in anatomical and physiological CSA’s (Klein, et al., 2001).

2.3. Muscle fiber length

Among architectural parameters of the skeletal muscle, fiber length are particularly important because the force exerted by muscle fiber is determined by its length (force-length relationship) (Gans, 1982). Long fibers can shorten at faster speed than short fibers, so that fiber length affects the force-velocity relationship as well (Kawakami and Fukunaga, in press). In the present study, we regard fiber and fascicle lengths as identical, which has been shown in pennate muscles with short fibers such as the triceps surae (Kawakami, et al., 2000b).

There is some evidence from animal studies concerning the plasticity of muscle fiber length. Immobilization of quail muscle in a stretched and loaded condition increased both CSA and the length of muscle fibers (Alway, et al., 1989; Friedrich and Brand, 1990; Huijing, 1985; McComas, 1996; Wickiewicz, et al., 1983; Yamaguchi, et al., 1990). Recently, fiber length measurement has been carried out in vivo through imaging techniques such as MRI (Scott, et al., 1993) and ultrasonography (Kawakami, et al., 1995, 1998, 2000a, 2000b; Kumagai, et al., 2000; Rutherford and Jones 1992). By this technique, it has been possible to study the inter- and intra-individual differences in fiber length. The fiber lengths of the triceps surae muscles exhibit a large variability among individuals, and they are not correlated with lower leg lengths (Chow, et al., 2000). Cadaver observations have also provided variable muscle fiber lengths among individuals (Murray, et al., 2000). These findings suggest the question of whether muscle fiber lengths are genetically determined or altered after birth. Abe, et al. (2000) found longer fascicle lengths in sprinters than in long distance runners. Long fascicle lengths correlated with sprint performance both in women and men (Abe, et al., 2001; Kumagai, et al., 2000). These findings confirm the inter-individual variability in fascicle or muscle fiber length, suggesting once again the possibility that fiber length is altered by specific training, which warrants further longitudinal studies.
3. Functional consequences of architectural changes in skeletal muscle by strength training

3.1. Force transmission from muscle fibers to tendon

The pennation angle determines the transmission of muscle fiber force to tendon (Gans and de Vree, 1987; Wickiewicz, et al., 1983). Alexander and Vernon (1975) predicted from a simple planimetric model of a pennate muscle that an increase in pennation angle results in muscle force enhancement by virtue of an increment in physiological CSA, though pennation angles above 45˚ cause a detrimental effect for a decrease in muscle force (Figure 4). Previously, it was believed that changes in fiber pennation, if any, would not be a major determinant of changes in force generation as a result of strength training (Jones, et al., 1989). One of the rationales for this belief was a relatively small (~20˚) pennation angle in human cadavers (Alexander and Vernon, 1975). However, as described above, it is now widely accepted that muscle hypertrophy accompanies an increase in pennation angles reaching as much as 55˚ (Kawakami, et al., 1993, 2000a). Therefore, the influence of pennation angle increase on muscle fiber force transmission might be substantial. Hypertrophied muscles with large pennation angles, therefore, might have disadvantageous force-producing capacities, as evidenced by a decrease in specific tension.

3.2. Specific tension

Muscle strength is known to be a linear function of size (e.g. CSA) (Gadeberg, et al., 1999; Ikai and Fukunaga, 1968; Maughan, et al., 1983; Roy and Edgerton 1992; Sale, et al., 1987). This is because muscle fiber force is closely related with CSA (Close, 1972). The specific tension, i.e., muscle force relative to physiological CSA, is fairly constant, regardless of its fiber type compositions (Nygaard, et al., 1983; Spector, et al., 1980). Although there are some studies reporting fiber-type dependence of specific tension (e.g., Powell, et al., 1984), it has been pointed out that the variation in the specific tension between different fiber types is due to methodological errors in assessing fiber CSA (Eldred, et al., 1993). The predictability of muscle force generating capability from muscle size, however, is questioned since it has been shown both in animals and in humans that there are training-induced changes in specific tension. Apart from possible changes in

Figure 4  Positive and negative effects of pennation angles (based on Alexander & Vernon, 1975). As the pennation angle increases, the physiological cross-sectional area (PCSA) increases, but force transmission from muscle fibers to tendon decreases. These two factors result in an overall effect.
neural activation or drive to muscle force generation (Aagaard, et al. 2000; Jones and Rutherford, 1987; Ploutz, et al 1994; Sale, 1988; Kitai and Sale, 1989; Sale and MacDougall 1981) and biochemical malfunction in hypertrophied muscles (Kandarian and Williams, 1993), recent studies have shown that strength training alters muscle architecture as described above, which could affect the linearity in the relationship between muscle size and strength. As described above, an increase in pennation angles can lead to a muscle force deficit due to a reduced muscle fiber force being transmitted to tendon. In other words, the disadvantageous effect of pennation (less efficient force transmission from muscle fibers to tendon) may be further amplified after strength training. This might explain the large deviation of reported specific tensions in human muscles (An, et al., 1989; Ikai and Fukunaga, 1968; Kawakami, et al., 1994; Narici, et al., 1989). Maughan, et al. (1983) demonstrated an inverse relationship between muscle CSA and the ratio of muscle strength to muscle CSA and suggested that in larger muscles pennation angles might be greater, resulting in a smaller strength-to-CSA ratio. Ikegawa, et al. (1994) and Kawakami, et al. (1995) have shown that this can actually be the case.

4. Future perspectives

It is now clear that muscle architecture changes through strength training, with the changes being sometimes well beyond previous expectations. The importance of muscle architecture in muscle functions, therefore, cannot be overemphasized, and studies on training (and detraining) responses should thus take into consideration architectural changes in the muscles involved. Before concluding the present review, I will summarize recently emerging ideas that should also be taken into account in discussions of muscle architecture in humans and some future perspectives.

4.1. Intra-muscle differences in muscle architecture

Muscle fiber length, pennation angles and other architectural parameters are often studied at a certain position within a muscle (e.g., at muscle belly) (Aagaard, et al., 2001; Abe, et al., 2000; Fukunaga, et al., 1997; Kawakami, et al., 1993). However, there might be architectural variability within a muscle. In this regard, previous studies are not in agreement, with some studies on human cadaver specimens showing fiber length variability (Huijing, 1985; Scott, et al., 1993) and others reporting identical muscle fiber length throughout muscle (Friedrich and Brand, 1990; Scott, et al., 1993; Wickiewicz, et al., 1983). Kawakami, et al., (2000a) studied intramuscular variation in fascicle arrangement of the human gastrocnemius muscle in vivo. They reported fairly uniform muscle fiber lengths both at rest and during isometric contraction at 50% of the maximal level. The magnitude of shortening of fibers upon contraction (30 - 34 %) was identical. On the other hand, pennation angles differed significantly at different positions.

Muscle fibers are arranged in a three-dimensional space (Lam, et al., 1991; Otten, 1988; Scott, et al., 1993). Because of this, the possibility of misevaluation of muscle fiber length and pennation angles exists. A recent study revealed a potential source of error in determining pennation angles and muscle fiber lengths (Kurihara, et al., 2005). If there is deviation between the plane of the ultrasound image and that of fibers, fiber lengths are underestimated and pennation angles are overestimated (Kurihara, et al., 2005). This error can be avoided by assuring a proper plane that is parallel to fibers and perpendicular to the aponeuroses onto which fibers are attached, but it is not always possible with the conventional two-dimensional ultrasonography. Thus, for accurate evaluation of architectural parameters, the three-dimensional imaging technique (e.g., 3D-ultrasonography) should be used. In addition, a recent study has shown inhomogenous activity within a muscle (Kinugasa, et al., 2005), which may also alter internal fiber architecture if such activity persists throughout training. Future training studies will reveal changes in three-dimensional fiber architecture as a result of strength training.

4.2. Changes in muscle architecture upon contraction

Because pennate muscles have long tendinous tissues, there is a large amount of muscle-tendon interaction, and muscle fibers shorten even during isometric contractions. This internal fiber shortening results in an increase in pennation angles which
reaches up to 70° in the medial gastrocnemius during maximal contraction even in non athletes (Kawakami, et al., 1998, Figure 5). Thus, the effect of pennation angles on muscle force production, and the functional impact of their increase, may be much greater than previously thought. The magnitude of muscle-tendon interaction varies among individuals (Kawakami and Fukunaga, in press), and it changes as a result of strength training (Kubo, et al., 2002). Therefore, even if there is no apparent architectural change after training in a resting muscle, there is high probability for altered pennation angles and muscle fiber lengths during contraction, which should be tested in future studies.

References

Figure 5 Ultrasonic image of the gastrocnemius muscle at rest (top) and during maximal isometric contraction (bottom). One fascicle is highlighted by a straight line. Left, distal, right, proximal.


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