Are muscles mechanically independent?

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Most physiology texts imply that the mechanism by which force is transmitted from sarcomeres to muscle insertions is simple: when skeletal muscles contract, cross-bridge forces are transmitted along myofibrils, through the sarcolemma and extracellular matrix to tendons and, ultimately, bones. At each level of organization, myofibrils, muscle fibers, and muscles behave as mechanically independent force generators. Muscle fiber tension is the sum of the tensions generated by individual myofibrils, muscle tension is the sum of the tensions generated by individual fibers, and the torque generated at a joint is the sum of torques produced by individual muscles crossing the joint.

In the last two decades most of this simple picture has come under suspicion, or been shown to be wrong (3, 9–11). Myofibrils transmit force not only longitudinally, but also to adjacent myofibrils and the sarcolemma. Muscle fibers transmit force not only to tendon, but also to adjacent muscle fibers and in-series fibers. Tendons are arranged partly in series and partly in parallel with muscle fibers. And, perhaps most surprisingly, it has been claimed that muscles transmit force not only through their own tendons, but also to adjacent structures, including other muscles.

Transmission of force from muscles to adjacent nonmuscle structures has been called “extramuscular myofascial force transmission.” Transmission of force from muscles to adjacent muscles has been called “intermuscular myofascial force transmission.” The collective term for extramuscular and intermuscular myofascial force transmission is “epimuscular myofascial force transmission” (5). To avoid presuming a mechanism, we refer to transmission of force between muscles as “intermuscular force transmission.”

Intermuscular force transmission implies that two muscles are not mechanically independent. That is, it implies the muscles are arranged in series (or partly in series and partly in parallel) and that their joint torques sum nonlinearly.

One view holds that intermuscular force transmission is ubiquitous and significant (5). If true, this would have important implications for muscle physiology. It would imply that the neural regulation of force is more complex than previously thought and that previously ignored mechanisms of muscle adaptation and pathophysiology need to be revisited. Significant intermuscular force transmission would also present a major impediment to biomechanical modeling of muscles.

Many structures provide potential anatomic substrates for intermuscular force transmission. Most obviously, some muscles (such as triceps surae in some species) share common tendons. Occasionally, the tendons of one muscle branch and connect to adjacent tendons. An example is the vincula longa, which in humans connects flexor digitorum superficialis to flexor digitorum profundus. Last, an extensive network of “myofascial” connective tissue envelopes and connects muscles to each other (1, 2, 6). These structures provide a potential pathway for the transmission of force between muscles. It is also theoretically possible that intermuscular force transmission could occur even in the absence of connecting structures if muscles generated significant frictional forces when they moved relative to each other.

In the last decade, one productive laboratory in the Netherlands has reported many cleverly designed experiments investigating epimuscular force transmission (for review, see 5). The experiments were conducted on muscle preparations in which, as far as possible, myofascial connections were preserved. The following observations support the existence of epimuscular force transmission: 1) force measured at a muscle’s proximal tendon does not always equal the force measured at its distal tendon (6, 8); 2) surgical isolation of a muscle, which frees the muscle from its myofascial connections, changes the muscle’s length-tension properties and abolishes differences between forces measured at proximal and distal tendons (6); and 3) changes in the length of one muscle change the length-tension properties of a second muscle (8).

These observations provide evidence of epimuscular force transmission, but only the last observation provides evidence of intermuscular force transmission. That is, only the last observation demonstrates that force is transmitted from one muscle to another.

There are reasons to be concerned about the physiological relevance of these findings. Under physiological conditions, muscles are displaced relative to other structures (2). The significance of intermuscle displacements is that they determine the strains experienced by myofascial tissue, and therefore also (if intermuscular force transmission is mediated by myofascial connections) the magnitude of intermuscular force transmission. A major criticism of the observations used to demonstrate intermuscular force transmission is that it is not clear that they were made within usual physiological ranges of displacements between muscles and other structures.

In a study in the Journal of Applied Physiology, Maas and Sandercock (8a) describe an alternative approach to test the importance of intermuscular force transmission. For the primary experiment, they used a cat hindlimb preparation in which the myofascial network remained nearly completely intact. They showed that changing the knee angle did not influence the ankle torque produced by selective stimulation of the soleus muscle. (Changing the knee angle changes the length of the gastrocnemius, but not the soleus.) These data suggest there is little or no intermuscular force transmission between the cat gastrocnemius and soleus muscles at physiological lengths.

Maas and Sandercock’s approach was to leave the gastrocnemius and soleus muscles’ insertions attached and to change muscle lengths by manipulating the position of the ankle and knee. With this approach the displacements between the resting gastrocnemius and soleus muscles were necessarily within the ranges that occur in vivo, and thus this experimental prepara-
tion was probably more physiologically relevant than previous ones. Nonetheless, the physiological relevance of Maas and Sandercock’s findings are still open to question because the protocol involved tetanic stimulation of the soleus muscle while the gastrocnemius remained quiescent. In this respect the experimental observations were nonphysiological: we are not aware of any motor tasks in which the soleus is activated maximally while the gastrocnemius remains relaxed. It may be that isolated tetanic stimulation of the soleus muscle causes nonphysiological displacement of soleus relative to gastrocnemius. Thus Maas and Sandercock’s observations, like earlier observations, are vulnerable to the criticism that the intermuscular displacements were nonphysiological.

It is not yet known if the new findings on cat gastrocnemius and soleus can be generalized to other muscles. However, there is reason to expect intermuscular force transmission between other muscle pairs would be no greater than between the gastrocnemius and soleus. The gastrocnemius spans two joints, whereas the soleus spans just one, so myofascial connections between the gastrocnemius and soleus would probably experience greater strains than the connections between pairs of single-joint muscles. These speculations notwithstanding, it would be instructive to replicate Maas and Sandercock’s experiment with other muscles and in other species, including humans.

Other observations, on humans in vivo, suggest intermuscular force transmission is normally negligible. We have shown that changes in length of the muscle fascicles in the human medial gastrocnemius associated with a particular change in muscle-tendon length are not influenced by whether the change in muscle-tendon length was produced by movement at the knee or ankle (4). Another relevant observation is that during a static grasp involving all digits, the force produced by single motor units in the flexor pollicis longus shows minimal (~5%) spread to the adjacent flexor digitorum profundus (12). A similar conclusion can be derived for force transmission between compartments of multitendoned muscles such as extensor digitorum communis (e.g., Ref. 7). These data support the contention that there is normally little or no transmission between human muscles in vivo.

REFERENCES