More than Meat and a Motor: The Diverse Biomechanical Roles of Skeletal Muscle and Their Place in ‘Semi-Living’ Machines

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Abstract

The biomechanical roles of skeletal muscle and their tendons are diverse. Perhaps most intuitively, muscle is regarded as a biological ‘motor’ that provides the work required for accelerating the body and overcoming aero- and hydrodynamic forces. With detailed biomechanical analyses, more intricate roles of the muscle-tendon unit have been uncovered, ranging from energy recyclers, to shock absorbers and capacitors. The functional scope of muscle-tendon tissue makes it an attractive choice for exploring bio-machine integration. Research and cross-disciplinary collaboration at SymbioticA offers a testbed for scientific and artistic exploration into engineered muscle-tendon constructs and the broader philosophical debate surrounding their place in ‘semi-living’ machine systems.

Biomechanical Roles of Muscle and Tendon

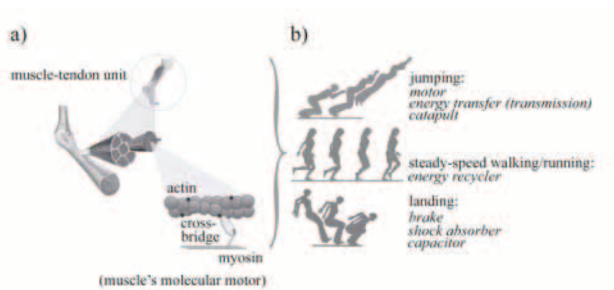
A motor

When asked what mechanical function muscle plays in animal movement, most will answer that it provides the work required to move. Indeed, skeletal muscle can be seen as a molecular motor. It is composed of two myofilaments, actin and myosin that, when activated, form crossbridges (Fig. 1) that convert chemical energy (ATP) into mechanical work. A single crossbridge produces on the order of $30 \cdot 10^{-21}$J of work and ~ 10^{-22} W of power [1]. Whilst a single crossbridge can hardly produce useful movement, when combined, the ~ 10^{14} crossbridges per mg of skeletal muscle produce truly impressive work and power output, for instance hovering by hummingbirds (~120 W/kg sustained muscle power!) or, to use a human example, world-record high jumps in excess of 2m.

A brake

By investigating the *in vivo* forces and lengths of individual muscles during animal locomotion it has become apparent that not all muscles function as motors to produce work. Some muscles primarily absorb energy and thus effectively function as a brake. Humans, birds and cockroaches are some of the animals that employ muscle brakes during steady-speed running [2-4]. Human hamstring muscles (and presumably those of other animals) function as a brake to decelerate the swinging leg during walking and running. This same limb-swing brake mechanism has been exploited for human purposes; Donelan and colleagues’ wearable clutch-enabled knee brake not only mitigates the need for the biological muscle brake during walking, their clever design also includes an electrical generator capable of recharging cell phones and other devices [4].

Fig. 1. (a) Hierarchy of muscle organization; (b) examples of common locomotor tasks and the biomechanical roles of muscles to achieve them. For more extensive reviews see [5,8]. (© Jonas Rubenson)



Energy recycling and transmission

There are other instances during animal locomotion when muscle fibers actively produce force but shorten or lengthen minimally (isometric strut). The human calf muscles and the analogous muscles in turkeys, wallabies, and other animals function in this manner during walking and running [5], and it is instead the Achilles tendon spring that stretches and recoils during the step that provides mechanical work. The energy required to stretch the tendon comes from the transient fluctuations of the kinetic and potential energy of the body. This form of energy recycling reduces the work required by muscle fibers, saving metabolic energy. The ostrich, one of the most economical runners measured to date, owes its high running economy to its 80cm long springy toe tendons [6]. Muscles functioning as struts also have a role in energy transmission. The bi-articular gastrocnemius (calf) muscle is known to transfer the power generated by the large knee extensors (quadriceps) distally to the ankle during the acceleration phase of running and jumping [7]. Muscle transmission helps to redistribute and control the power between the different leg joints.

A catapult

Some animals are capable of very high bursts of power production. For example, jumping birds, frogs, and the small primate *Galago Senegalensis* (Bushbabies) generate up to 800, 1600 and 2400 W/kg muscle during jumping, respectively [8]. These levels of power production outstrip the power capacity of skeletal muscle (set by the muscle’s cross-bridge dynamics and force-velocity properties) by nearly an order of magnitude. These exceptional levels of power are achieved by muscles slowly stretching a tendon (low power) followed by a rapid release of the stored tendon elastic energy (high power), similar to that of a catapult. This amplification of muscle power is possible because the tendon’s collagen structure does not have the same biomechanical limitations of muscle.

Shock absorbers and capacitors

Some muscle-tendon units in animals specialized for fast and economical running have very short fibers attached to very long tendons. For example, the superficial and deep digital flexor muscles of the horse are no more than ~5mm, but their tendons are 75cm long. The tendons from these muscles are ideal for recycling energy during the gait cycle (see above), but the role of the muscle fibers themselves is less clear. Rather than function as actuators, these muscle fibers may have a more important role in damping the high frequency oscillations that occur in the bony limb structures during running and galloping [9] and are key for reducing tissue fatigue damage related to high frequency vibrations. Tendons also have a shock absorbing function in animal movement. To rapidly decelerate the body, for instance during landing from a jump, muscles must dissipate energy. This is achieved by muscles absorbing energy, but when done rapidly under high loads this places the muscle at risk of lengthening (eccentric) damage. Much like a capacitor, tendons attached to muscles are able to decrease the rate of power absorption by the muscle and to temporarily delay its onset [6].

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Engineered Muscle as a 'Semi-Living' [10] Machine

The versatility of muscle as a biological machine makes it a particularly attractive tissue for exploring biological integration in synthetic devices and human-machine interfaces. In addition to its diverse mechanical capabilities described above, muscle tissue has, as outlined by Herr and Dennis [11], several additional attributes; it relies on a biocompatible fuel, it can adapt to the mechanical environment (e.g. grow or shrink under various load requirements), it can repair itself, it has a built-in sensory system, and owing to it's inherent inefficiency it can even provide a source of heat.

The research at SymbioticA, most recently the 'Tissue Engineered Muscle Actuator (TEMA)' project, offers a test-bed to explore, both scientifically and artistically, the interplay between biological muscle tissue and its diverse functions, and synthetic systems. It also serves to open up important debate around the ethical and philosophical issues surrounding muscle bio-machine interfacing.

'Semi-living' muscle tools and art forms

At a basic science level, questions surrounding the biological function of engineered muscle-tendon constructs are possible. For example, can an explanted or cultured muscle perform any/all of the diverse biological roles outlined above, and to what effect? Can a biological muscle-tendon unit be interfaced with a simple machine to control movement (e.g. actuator) or loading environment (e.g. shock absorber)? Recent work using explanted frog muscle shows promise for the use of skeletal muscle as a controllable actuator for robotic systems [11,12]. Furthermore, what 'training' conditions are required for optimal muscle-tendon function, and can an integrated engineered muscle-tendon unit adapt to its environment? The combination of muscle tissue engineering with a complementary program on tendon tissue engineering [13] provides a unique framework for designing complete engineered biological muscle-tendon-unit constructs on which the above questions can be examined (Fig. 2).

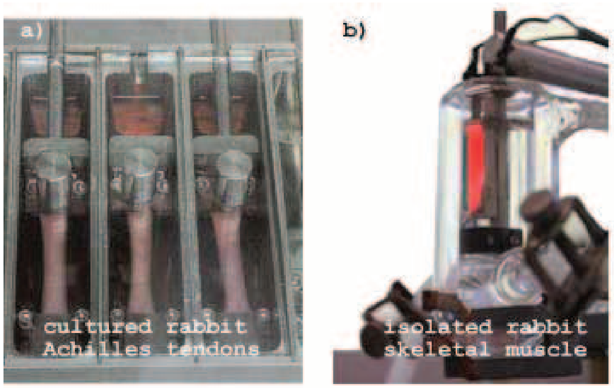

Fig. 2. (a) Bioreactor for tendon culture [13]. (© Jonas Rubenson. Photo: Tao Wang.) (b) Isolated (rabbit) muscle preparation for machine interfacing. (© Jonas Rubenson)

In a broader cultural context, will future hybrid bio-machine tools be regarded as 'alive'? A prosthetic device instrumented with a cultured muscle tissue actuator might indeed be interpreted as a living component of its wearer. At what level then is a tissue-engineered muscle actuator designed for human purposes different from our initial (and since abandoned) use of biological muscle actuation in human technology, namely the use of oxen and horses (muscle) to plough fields (as early as ~6000 BC [14])? It is also not clear whether perceptions of 'semi-living' would extend to situations where engineered muscle is adopted for less intuitive and more static functions, for example as dampers that remove unwanted vibrations rather than actuators that produce movement.

If it is movement that evokes a sense of vitality, the fact that a hybrid bio-machine moves under its own biological power may, indeed, further heighten perceptions of life. By designing simple mechanical and control interfaces between muscle actuators (both explanted and tissue engineered) and external devices and the environment, the TEMA project can explore the complex intersection between the semi living machine, movement and the observer (Fig. 2). Finally, there is the uneasy question of whether these engineered muscle machines and cultural objects might also fulfill the other prominent role carried out by their natural biological counterpart: meat!

References and Notes

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Glossary

crossbridge - the chemical bonding of the myosin head to actin.

myofilament - the contractile filaments of skeletal muscle, comprised of the thick filament, myosin, and the thin filament, actin.