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Animal locomotion research: achievements and perspectives

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Biomechanics is helping us to understand all kinds of animal locomotion, from the crawling of worms and the swimming of jellyfish to the flight of birds. Much of our understanding of human movement had its origins in research on animals.

Human walking is unique; no animal walks as we do. However, research on hopping kangaroos has revealed basic principles that apply as much to running as to hopping, and to humans as to animals. Early work using simple methods showed how energy is saved by the elasticity of tendons. More recent research using sonomicrography and ultrasonic imaging has shown how some leg muscles may remain almost isometric while their tendons stretch and recoil. Repeated stretching under high stresses may result in fatigue damage and overheating in leg tendons of running animals.

Early research on animal swimming and flight used conventional hydrodynamics, as applied to aeroplane wings and helicopter rotors. This led to paradoxical results, failing for example to explain how some insects could generate enough aerodynamic lift to fly. This failure was due to the unsteady effects resulting from the continually changing angles and velocities of the wings. Understanding of these effects is growing rapidly, aided by digital particle image velocimetry (which reveals the patterns of flow that flying and swimming animals produce in the fluid around them) and by computational hydrodynamics.

One topic that has attracted a lot of attention recently has been the relationship between the properties of muscles and their behaviour in the intact animal. Here unsteadiness is again a problem, albeit in a different way. Conventional force-length and force-velocity experiments cannot by themselves explain what happens in rapid cycles of lengthening and shortening. Work loop experiments, simulating in vitro the muscle's in vivo behaviour, are giving increased but far from complete understanding.

Where applicable, the authors confirm that the experiments described here conform with the Physiological Society ethical requirements.

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Predicting the maximum mechanical power of muscle-tendon units

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Muscles contain elastic material, both intracellular and extracellular, which is mechanically in series with the crossbridges, which are the force generators. When force increases energy is stored in these structures. The work that a muscle produces in a given period is a therefore combination of the power generated by the crossbridges themselves during this time and any change in the amount.of energy stored in the series elastic material. Since the energy stored elastically is determined by the force in the stored elasticity there is no change in stored work when the force is constant.

Constant force

The simplest case for which the power output might be predicted is a period of constant force. If the period is long enough the classic force velocity curve applies. Maximum power can be expressed as a function of the maximum shortening velocity, the maximum force and the curvature of their relation. Both maximum power and maximum velocity increase with increasing temperature. Maximum power increases very steeply with temperature. There are major differences between vertebrate species in the maximum power at a given temperature. In part these can be understood as adaptations to the different physiological temperatures. Skinned, or permeabilised muscle fibres generally have reduced power output compared to intact muscle fibres. This may be due to raised ADP level.

During brief intervals of shortening under constant force following from isometric contraction higher power output is possible than the force velocity curve predicts Presumably this is because work is provided by a change in the distribution of crossbridge states during this period.

Series elasticity and inertial load

If a muscle is connected to an inertial load and then activated the power output will rise above the maximum predicted by the force velocity curve. This is because work stored in the series elasticity early in the contraction is later released. There is a clear limit to the extra power that can be obtained in this way. This limit can be exceeded if the load is connected to the muscle via a cam, or is restrained by a catch. With these mechanical arrangements there is no clear theoretical limit to how much power can be delivered, although the work that can be delivered is limited simply by the compliance of the series elasticity.

Work stored in crossbridges

When a muscle is stretched work is stored not only in the series elasticity but also in the contractile machinery itself. This work decays into heat with a time constant of about 50 ms, but may be available to enhance power output while it remains.

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Biomechatronics: merging body and machine

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Rehabilitation technology is at the threshold of a new age when orthotic and prosthetic devices will no longer be separate, lifeless mechanisms, but will instead be intimate extensions of the human body - structurally, neurologically and dynamically. Such a merging of body and machine will not only increase the acceptance of the physically challenged into society, but will also enable individuals suffering from limb dysfunction to more readily accept their new artificial appendages as part of their own body. Several scientific and technological advances will accelerate this mergence, including the development of actuator technologies that behave like muscle, control methodologies that exploit principles of biological movement, and device architectures that resemble the body's own musculoskeletal design.

In this lecture, I first discuss how leg muscles and tendons work mechanically during walking in order to motivate the design of efficient orthotic and prosthetic limbs. I hypothesize that a prosthetic leg comprising only knee and ankle quasi-passive elements, including springs, clutches and variable-damping components, can capture the dominant mechanical behavior of the human knee and ankle during level-ground ambulation. As a preliminary evaluation of this hypothesis, I put forth a simple model that captures the gross features of the human musculoskeletal leg architecture. Model predictions are in good agreement with experimental gait data, suggesting that knee and ankle motors are not necessary for level-ground prosthetic leg ambulation. This result is in support of the idea that muscle-tendon units that span the human knee and ankle mainly operate as tunable springs in walking, affording the relatively high metabolic walking economy of humans. The result also highlights the importance of agonist-antagonist actuation and polyarticular limb architectures in the design of efficient, low-mass, and quiet legged systems for walking.

In addition to orthotic and prosthetic biomimetic leg design, the lecture emphasizes the importance of harnessing both zero-moment and moment balance control strategies for the enhancement of bipedal stability and dynamic cosmesis. Recent bipedal walking controllers have included the capability of controlling angular momentum explicitly (Yokoi et al. 2001; Sugihara et al. 2002; Nisiwaki et al. 2003; Popovic et al. 2004; Komura et al. 2005). Many of these controllers tightly regulate angular momentum to be zero at all times. While this is consistent with human behavior during normal walking, such a high level of regulation is not always desirable. For example, when foot placement is constrained, it is often necessary to temporarily sacrifice goals of regulating angular momentum in favor of the more important goal of maintaining balance. In the lecture, I discuss situations where angular momentum should not be zero, and I present a controller that automatically integrates moment-inducing balance strategies with non-moment strategies. The controller uses a multi-variable optimal control approach to automatically balance competing goals for translational and angular momentum. Performance limits of the controller are presented, and compared with those of human test subjects. The lecture concludes with a general discussion of the importance of biologically-inspired hardware and control architectures in the implementation of highly functional legged systems for prosthetic, orthotic and robotic applications.

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