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Phil. Trans. R. Soc. B 2011 **366**, 1463-1465

doi: 10.1098/rstb.2010.0354

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Introduction

Mechanics, modulation and modelling: how muscles actuate and control movement

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Animal movement is often complex, unsteady and variable. The critical role of muscles in animal movement has captivated scientists for over 300 years. Despite this, emerging techniques and ideas are still shaping and advancing the field. For example, sonomicrometry and ultrasound techniques have enhanced our ability to quantify muscle length changes under *in vivo* conditions. Robotics and musculoskeletal models have benefited from improved computational tools and have enhanced our ability to understand muscle function in relation to movement by allowing one to simulate muscle–tendon dynamics under realistic conditions. The past decade, in particular, has seen a rapid advancement in technology and shifts in paradigms related to muscle function. In addition, there has been an increased focus on muscle function in relation to the complex locomotor behaviours, rather than relatively simple (and steady) behaviours. Thus, this Theme Issue will explore integrative aspects of muscle function in relation to diverse locomotor behaviours such as swimming, jumping, hopping, running, flying, moving over obstacles and transitioning between environments. Studies of walking and running have particular relevance to clinical aspects of human movement and sport. This Theme Issue includes contributions from scientists working on diverse taxa, ranging from humans to insects. In addition to contributions addressing locomotion in various taxa, several manuscripts will focus on recent advances in neuromuscular control and modulation during complex behaviours. Finally, some of the contributions address recent advances in biomechanical modelling and powered prostheses. We hope that our comprehensive and integrative Theme Issue will form the foundation for future work in the fields of neuromuscular mechanics and locomotion.

Keywords: muscle architecture; simulation; muscle mechanics; locomotion; musculoskeletal modelling

Locomotion involves the propulsion of an animal's body in air, on land or in water, and is studied by scientists from numerous fields, ranging from evolutionary biology to bioengineering [1]. Beginning with key observations made by Aristotle, locomotion has been the subject of great interest for over two millennia. Borelli [2] contributed pioneering studies of both fin-based locomotion as well as mechanical models of limbed locomotion. Marey [3] conducted some of the first experiments (without electronics) on terrestrial and aerial locomotion, presaging many of the experimental questions scientists have addressed in recent decades. Locomotion emerges from the integration of multiple active and passive structures. For example, active muscle can generate force to stretch tendons and move skeletal elements. For dynamic movement

to be effective, sensory feedback is integrated and alters the motor output that controls movement of the body or appendages (e.g. wings, legs or fins). Locomotion is extremely diverse and suites of constraints and attributes that dictate the underlying mechanisms of movement accompany different patterns of locomotion.

Muscles are vital for driving animal movement over a range of conditions [4]. Although movement can be relatively simple, the actions of underlying muscles are often complex and can be altered depending on the habitat conditions [4,5]. This variation can be in the form of neural control, muscle strain or muscle force. Linking this variation in muscle function to dynamic changes in demand is a necessary step for muscle biologists trying to understand the mechanisms underlying natural movements, and is a departure from the majority of studies that examine muscle function under relatively steady or quasi-static conditions [6,7]. A rich history of experimental work has examined how muscles work and, specifically, how they drive

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One contribution of 15 to a Theme Issue 'Integration of muscle function for producing and controlling movement'.

locomotion. Muscles are considered actuators when they shorten or lengthen to produce or absorb energy, doing mechanical work. In other instances, muscles may do little work but can facilitate elastic energy storage and return or help to stabilize a joint. The emergence of sophisticated techniques used to quantify *in vivo* muscle function, such as sonomicrometry and ultrasound, and improved and more accurate musculoskeletal models incorporating detailed information regarding muscle architecture [8] are enhancing our ability to study the dynamics of the muscle. Given the recent, and influential, advances that have taken place with regards to muscle function, the goals of this Theme Issue are to (i) highlight our current understanding of how muscles actuate and control movements, (ii) describe how muscles function in a variety of animals and movement conditions, and (iii) detail the techniques and models used to simulate muscle function under time-varying conditions.

The first paper in our Theme Issue addresses the relationship between skeletal muscle design and movement [9]. In particular, the authors highlight important examples where muscle architecture and arrangement can enhance performance. For example, Lieber & Ward discuss trade-offs between force and velocity, benefits of biarticular muscles and the relationships between moment arms and fibre lengths during movement. The second paper addresses regional variation in architecture and function within muscles, but also intermuscular force transmission between muscles of different limb segments [10]. Specifically, the authors assess the prevalence of variation in fibre type, strain and force within single muscles, and whether this might have a functional benefit to the animal. Higham & Biewener also assess how proximal and distal hindlimb muscles in the guinea fowl can interact during locomotion by examining three muscles that are physically linked. They point out that, during part of the stance phase, the activity of proximal muscles might enhance the mechanical function of the more distal medial gastrocnemius.

The next group of three papers focuses on the roles of muscle in driving locomotion in diverse groups of animals, including frogs [11], birds [12] and fishes [13]. Roberts *et al.* [11] present new data to test whether muscle properties, such as available muscle power, can be used to predict jump distance in frogs. For three species, they quantify power during jumping using a force plate, and also quantify peak power output from the plantaris muscles of each species. They find no correlation between muscle power and jump power, and suggest that non-muscular mechanisms are the main reason for this. The next paper addresses muscle function in relation to avian flight [12]. In his paper, Biewener examines how the primary flight muscles, the pectoralis (downstroke) and supracoracoideus (upstroke), produce the considerable power required for active flapping flight. To accomplish this, these muscles are activated under isometric or stretching (eccentric) conditions and contract over a large strain range (approx. 35–40% of resting fibre length). Distal intrinsic wing muscles are much smaller, functioning to adjust wing aerodynamic properties by controlling wing shape. Syme & Shadwick [13] review locomotion in lamnid sharks

and tunas, but also present new data on *in vivo* muscle function in thresher sharks. They highlight the specializations for enhanced power output during swimming in lamnids and tunas, which include centralized, warmed locomotor muscle and long-reaching posteriorly directed tendinous structures. The red muscle is both deep and anterior, allowing the tendons to span large numbers of body segments. Using data from thresher sharks, they conclude that endothermy in fishes, and internalized red muscle, does not predict or dictate swimming mode.

The next two papers assess muscle function during human hopping [14] and walking [15] by employing simulation models of the musculoskeletal system. Bobbert & Casius [14] analyse a simulation of hopping and show that subjects activate their muscles to make smooth motions rather than to minimize energy expenditure. Arnold & Delp [15] combine experimental measurements of joint angles and muscle activation patterns during walking with a musculoskeletal model that captures the relationships between muscle fibre lengths, joint angles and muscle activation. Analysis of this model reveals that when musculotendon compliance is low (e.g. in hip muscles), the muscle fibre operating lengths are determined predominantly by the joint angles and muscle moment arms. If musculotendon compliance is high (e.g. in ankle muscles), muscle fibre operating length is more dependent on the activation level and force–length–velocity effects.

The next two papers assess how movement mechanics is related to the structure and function of the muscle–tendon unit [16,17]. Wilson & Lichtwark [17] provide an extensive overview of muscle and tendon function during locomotion by discussing activation timing and muscle length changes in relation to muscle architecture in humans, goats and horses. They also discuss the importance of elastic energy storage in tendons, and why it is important to tune the elastic energy return. Wakeling *et al.* [16] discuss the importance and mechanisms of variable gearing in muscles and how this relates to the coordinated recruitment patterns of muscles by examining the function of the triceps surae during human cycling. They point out that appropriate gearing translates into effective force and power production and good mechanical efficiency.

The next four papers assess the ability of the neuromuscular system to deal with changes in the environment, whether it be obstacles [18–20] or habitat transitions [21]. Daley & Biewener [18] examine the *in vivo* contractile dynamics of two distal leg muscles of the guinea fowl as they negotiate running over obstacles in relation to the muscles' function during steady-level locomotion. They show that the neuromechanical response of the lateral gastrocnemius and digital flexor muscles is context dependent. Activation of the lateral gastrocnemius increased for obstacle strides, indicating reflex modulation to increase work output. However, both muscles contracted at increased length and decreased shortening velocity, which provided a rapid intrinsic response to increases in muscle force and work output. Gottschall & Nichols [21] review the literature pertaining to transitions between level and hill surfaces, but they also present new data regarding the neuromuscular strategies for surface slope transitions. They find that

young adult cats can anticipate an upcoming transition to a hill by adjusting muscle activity as much as six steps prior to the transition. They find that muscle activity patterns and head pitch angles during anticipatory and transition strides are significantly different from level walking. Additional experiments assess how the vestibular system is linked to the muscle activity patterns, and conclude that neck proprioceptors, rather than vestibular organs, appear to initiate modifications in muscle activity patterns during surface slope transitions. The two papers by Sponberg *et al.* [19,20] assess the control potential of a single muscle in the cockroach, and how this control potential can shift owing to mechanical feedback. Not only is *in vivo* neuromuscular activity recorded, but the authors also manipulate the control of the muscle by adding spikes with stimulating electrodes [19]. They do this during both static (postural) and dynamic (running) behaviours. Under static conditions, the manipulation of neural control shows that stress develops linearly as muscle action potentials are added. The authors find that, during dynamics behaviours, the muscle can function to alter COM vertical impulse and body pitch, but can also control horizontal plane mechanics if the activation phase of the muscle is extended. In a complementary study, Sponberg *et al.* [20] develop a unique intact-joint workloop preparation by stimulating the muscle with bipolar extracellular electrodes while preserving the mechanical and physiological environment of the muscle. They ultimately test multiple hypotheses of muscle function to understand the control of posture and running in the cockroach. The muscle that they examine is found to change function depending on the task, similar to the context-dependent shifts in muscle function observed within the guinea fowl [18–20]. The muscle can absorb additional energy during swing, but acts as an effective motor during stance. These data ultimately reveal key aspects of the animal's neuromechanical control strategy.

The final paper of our Theme Issue assesses the function of a transtibial prosthesis and how it can be controlled by a neuromuscular model [22]. The controller produces speed adaptive behaviour; net ankle work increases with walking speed, highlighting the benefits of applying neuromuscular principles in the control of adaptive prosthetic limbs.

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