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Author for correspondence:
M. J. Schwaner
e-mail: mjschwan@uci.edu

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Not solely a motor: the role of muscles in sensory mechanisms and integrative control

M. J. Schwaner

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

MJS, 0000-0002-1666-3111

Muscles are widely appreciated as the main motors in movement, but their critical role as sensors in movement is often neglected. Locomotion requires precise yet flexible coordination of many muscles across multiple joints. Muscle activation patterns in rhythmic movements are coordinated by spinal neural circuits that include central pattern generator and proprioceptive feedback. Orchestrating the primary motor in movement—muscle—is a complex task because muscles must fulfil multiple mechanical functions, which influence how we move [1]. To coordinate mechanical roles with the precision timing required, muscles also act as proprioceptors to provide the nervous system with a sense of posture and motion. Muscle spindles are within-muscle somatosensory receptors that provide the body with this sense of proprioception. Spindle sensing properties are complex as they depend on the specific movement, forces and motor commands to the muscle. The effective integration of muscle mechanics and its sensory mechanisms is key to robust and adaptable locomotion. The sensing role of muscle is especially important under dynamic conditions, such as walking in rough terrain or recovering from perturbations, because the muscle's mechanical response depends on the dynamic interplay between the environment, intrinsic mechanics and sensory feedback (figure 1). Muscles require rapid and precise information about their state to effectively switch among the necessary mechanical roles in movement. Despite the apparent importance, the sensory role of muscle in proprioception in natural movements remains poorly understood.

A recent study by Kissane *et al*. [2] investigated the relationship between muscle spindle abundance, muscle architecture and movement dynamics. This study used a novel combination of individual-specific medical imaging and musculoskeletal modelling of the lower leg in human participants. Medical imaging was used to estimate muscle mass and fibre lengths, and to estimate muscle spindle density based on muscle mass and averaged literature data. The authors used the musculoskeletal models to estimate muscle work output and assign each muscle a mechanical role, based on each participant's individual kinematic and kinetic patterns during walking. The model analysis included a total of 23 individual muscles, spanning a range of estimated muscle spindle abundance. The authors found that the absolute number of muscle spindles was related to muscle fibre length, and predictive of total muscle length, its velocity profile, and to a certain extent to the force-generating capacity of muscles during walking [2]. Their findings suggest an intriguing correlation between muscle mechanical roles and spindle abundance. The authors concluded that muscles with higher estimated spindle densities operate predominantly as springs, whereas muscles with lower spindle abundance function as brakes during steady walking tasks. This work highlights the importance of integrated sensing and mechanical action for effective control of muscles in movement.

Studying the complex interactions between muscle morphology, sensing function and mechanics of movement during locomotor tasks is challenging because many features cannot be measured directly. While studies on human participants present many advantages and results have many important applications, there are important limitations on direct measures that can be made in human subjects due to ethical constraints. The study by Kissane *et al*. [2]

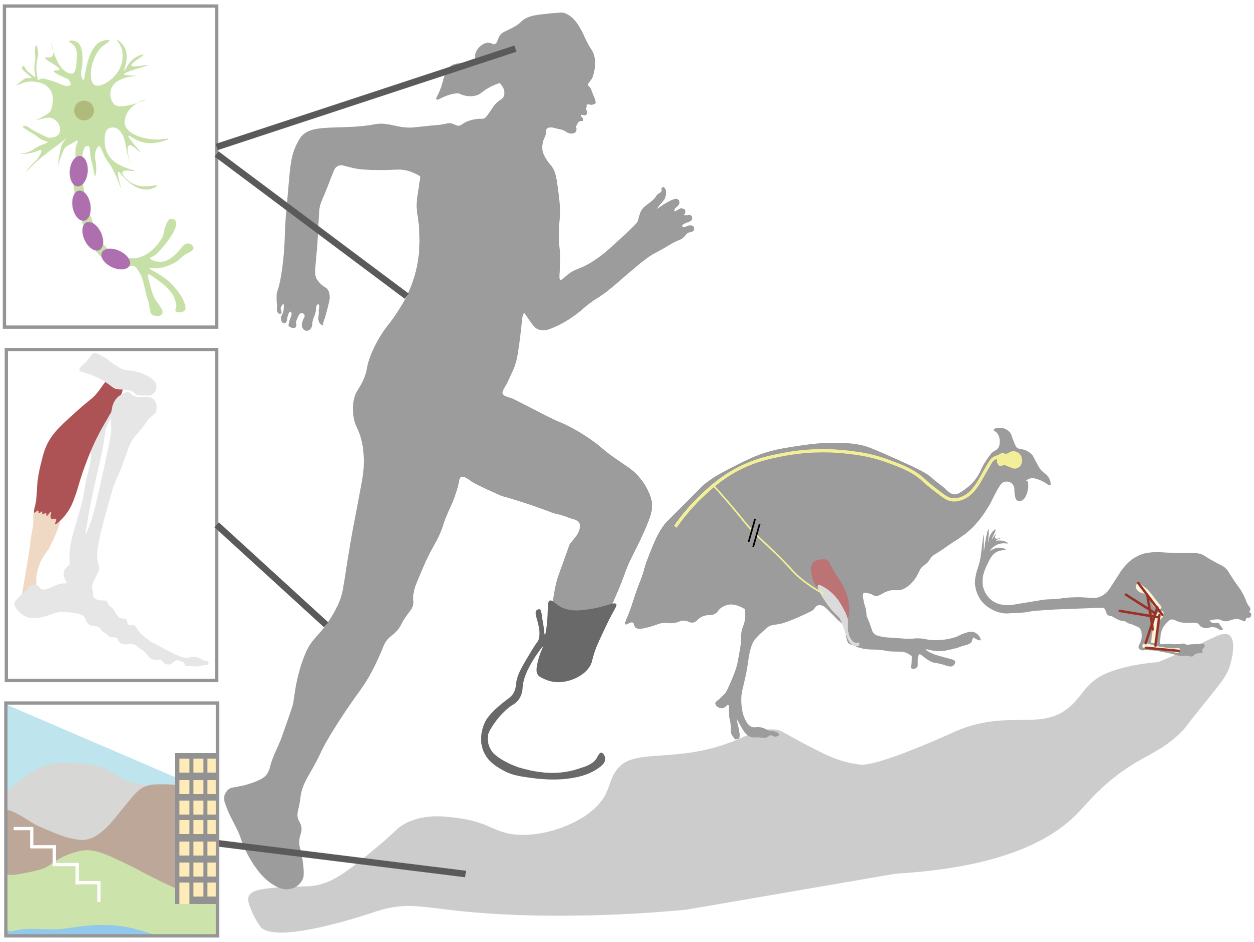

Figure 1. Navigating complex terrains requires dynamic interaction between the environment, the sensory system and the musculoskeletal system. Understanding the role of muscles—as actuators and sensory organs—among the diversity of animal locomotion, can act as a pool of inspiration for knowledge of fundamental principles of the physics of movement (and) for use in robotic devices. Important future directions include further exploration of experiments including smart prosthetic devices, *in vivo* muscle dynamics following nerve reinnervation procedures and musculoskeletal modelling approached. Figure is not to scale. (Online version in colour.)

estimated muscle spindle abundance because this could not be measured directly. Additionally, they focused solely on steady-state walking, which allows the simulation of muscle–tendon dynamics based upon non-invasive measures of anatomy and movement dynamics. However, the mechanical roles played by muscles and their sensorimotor responses likely differ during unsteady walking and in responding to postural disturbances. For example, distal leg muscles such as the triceps surae exhibit varied and complex mechanical function, operating more like a strut or spring in some parts of the gait cycle, with isometric contraction and elastic energy cycling in the Achilles tendon, but contributing as a motor to propel push-off at the end of stance in walking [3]. Additionally, this same muscle group can rapidly switch from strut-like function in steady tasks to transfer energy across joints, to damping function in response to a sudden increase in load [4,5]. This highlights the potential importance of the triceps for navigating complex terrains that require dynamic changes in function to facilitate robust and stable locomotion. Versatile switching among mechanical roles requires precisely timed modulation of neural control, yet a large gap remains in understanding how sensing and control dynamics are integrated to achieve mechanical function. The findings from Kissane *et al.* [2] suggest an important hypothesis about the relationship between a muscle's mechanics and spindle sensory organ abundance and highlight the importance of considering the relationships between muscle sensing and mechanics.

Nonetheless, important knowledge gaps remain in understanding how the nervous system and the body work together to coordinate robust and stable locomotion. Further advances in our understanding will require direct and dynamics measures of muscle mechanics and sensorimotor control. Kissane *et al.* present a unique, novel and cross-disciplinary approach which has the potential to further unravel the complexity of the relationship between muscle mechanics and sensory feedback [2]. Future dynamic measures can be facilitated by combining emerging technologies with established experimental approaches to understand how the individual elements of the system are integrated across organizational scales, from muscle fibres and contractile function, spindles and sensory signals to the coordination of dozens of muscles to achieve a stable walking gait. For example, *in vivo* measurements of muscle dynamics allow us to characterize dynamic muscle contraction patterns while navigating difficult terrain, which can help pinpoint how muscles rapidly switch among mechanical roles across different locomotor tasks. Surgical self-reinnervation procedures—resulting in a long-term deficit of proprioceptive feedback in the target muscle—are a useful tool to investigate neuromechanical control mechanisms in locomotion and have been used in combination with *in vivo* measurements [6]. Currently, most direct *in vivo* measures of muscle dynamics are made in animals using indwelling transducers, and these methods have been established for decades, but only more recently have such measures been enabled in human subjects using non-invasive ultra-sound measurements [7,8]. Additionally, experiments in animal models can also provide more direct measures of muscle spindle densities and firing patterns. Recently, Blum *et al*. [9] have shown that muscle spindle firing can be predicted during active and passive conditions, based on a biophysical model of contractile dynamics of intrafusal muscle fibres, using first principles including muscle–tendon interactions. By combining spindle recordings and *in vivo* measures of muscle mechanical function across carefully varied locomotor tasks, we can obtain a more direct insight into the relationship between sensing and actuation in musculoskeletal movement. Additionally, parallel experimental studies in animals and humans are now more feasible than in the past and could enable more thorough testing and validation of modelling studies. In turn, predictive models enable advances that are not possible in experiments by testing how movement dynamics are influenced by systematic variation in specific isolated subsystems and parameters that cannot be directly manipulated in experiments [10].

Another important avenue to further investigate sensorimotor mechanisms in locomotion is the use of robots as physical models. Physical robot models offer advantages because they can generate a desired locomotor behaviour with minimalistic designs that omit much of the biological complexity and therefore help identify the fundamental elements necessary to generate the observed features of movement dynamics [11,12]. For example, Othayoth *et al*. [12] highlight physical models of cockroaches to understand the problem of gap crossing and self-righting. They use visualizations to show that cockroaches exhibit stereotyped locomotor modes with stochastic transitions between modes that are strongly influenced by environmental interactions and the potential energy landscape. Like simulations, physical models are more amenable than to controlled parameter variation and hypothesis testing compared to intact biological systems, and physical models directly interact with the environment and therefore require fewer simplifying assumptions than simulations of the physics of the task [12]. In future efforts, it will be important to develop models that include both sensing and actuation dynamics and can be compared to independent experimental observations.

To understand agile locomotor behaviours, we need deeper understanding of how muscles act as both mechanical actuators (as motors, springs, dampers and struts) as well as sensory organs. Tasks such as navigating uneven terrain require rapid responses to variation in the interaction between the body and environment, enabled through our subconscious proprioceptive perception of movement. Fundamental knowledge of movement and proprioception dynamics in humans and animals is important for understanding functional changes with age, as well as informing clinical treatment and rehabilitation strategies for neuromuscular dysfunction following nervous system damage from stroke or diseases such as diabetes. Additionally, knowledge of control dynamics in biological systems has important potential to further advance the design and control of legged robots and devices such as powered exoskeletons and prosthetics [13]. Current robot control is mostly based on pre-defined intended trajectories, which underperform in complex terrains [14,15]. The fact that we cannot achieve robustly functioning robots with agile locomotor behaviour highlights critical knowledge gaps in our fundamental understanding of the sensorimotor processes that facilitate our motor skills. As stated by Feynman, 'What I cannot create, I do not understand' [11]. It remains a challenge at the frontiers of biology to understand how animals effectively integrate mechanics and control to achieve versatile and robust locomotion in complex environments. Likewise, it remains a challenge in engineering sciences to effectively replicate the performance of animals. Furthermore, understanding muscles as complex multi-tasking organs in movement is important for interpreting the remarkable diversity of musculoskeletal form and function among animals (figure 1). Yet, there is still a lot to discover about how animals crawl, flap, slither, run and/or soar through their environments, with the use of two or multiple legs, wings, body and tails. Understanding the diversity of animal locomotion can act as a pool of inspiration for knowledge of fundamental principles of the physics and neuromechanics of movement for use in robotic devices.

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References

1. Roberts TJ. 2002 The integrated function of muscles and tendons during locomotion. *Comp. Biochem. Physiol. A* **133**, 1087–1099. (doi:10.1016/S1095-6433(02)00244-1)
2. Kissane RWP, Charles JP, Banks RW, Bates KT. 2022 Skeletal muscle function underpins muscle spindle abundance. *Proc. R. Soc. B* **289**, 20220622. (doi:10.1098/rspb.2022.0622)
3. Clark WH, Pimentel RE, Franz JR. 2020 Imaging and simulation of inter-muscular differences in triceps surae contributions to forward propulsion during walking. *Ann. Biomed. Eng.* **49**, 703–715. (doi:10.1007/s10439-020-02594-x)
4. Hof AL, Van Zandwijk JP, Bobbert MF. 2002 Mechanics of human triceps surae in walking, running and jumping. *Acta Physiol. Scand.* **174**, 17–30. (doi:10.1046/j.1365-201x.2002.00917.x)
5. McGowan CP, Neptune RR, Kram R. 2008 Independent effects of weight and mass on plantar flexor activity during walking: implications for their contributions to body support and forward propulsion. *J. Appl. Physiol.* **105**, 486–494. (doi:10.1152/japplphysiol.90448.2008)
6. Gordon JC, Holt NC, Biewener AA, Daley MA. 2020 Tuning of feedforward control enables stable muscle force–length dynamics after loss of autogenic proprioceptive feedback. *eLife* **9**, e53908. (doi:10.7554/eLife.53908)
7. Gilles GB, Biewener AA. 2000 Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). *J. Exp. Biol.* **203**, 3547–3563. (doi:10.1242/jeb.203.23.3547)
8. Dick TJ, Arnold AS, Wakeling JM. 2016 Quantifying Achilles tendon force *in vivo* from ultrasound images. *J. Biomech.* **49**, 3200–3207. (doi:10.1016/j.jbiomech.2016.07.036)
9. Blum KP, Campbell KS, Horslen BC, Nardelli P, Housley SN, Cope TC, Ting LH. 2020 Diverse and complex muscle spindle afferent firing properties

emerge from multiscale mechanics. *eLife* **9**, e55177. (doi:10.7554/eLife.55177)

10. De Groote F, Falisse A. 2021 Perspective on musculoskeletal modelling and predictive simulations of human movements to assess the neuromechanics of gait. *Proc. R. Soc. B* **288**, 2020432. (doi:10.1098/rspb.2020.2432)
11. Aguilar J *et al.* 2016 A review on locomotion robophysics: the study of movement at the intersection of robotics, soft matter and dynamical systems. *Rep. Prog. Phys.* **79**, 110001. (doi:10.1088/0034-4885/79/11/110001)
12. Othayoth R, Xuan Q, Wang Y, Li C. 2022 Locomotor transitions in the potential energy landscape-dominated regime. *Proc. R. Soc. B* **288**, 20202734. (doi:10.1098/rspb.2020.2734)
13. Pfeiffer R, Lungarella M, Iida F. 2007 Self-organization, embodiment, and biologically inspired robotics. *Science* **318**, 1088–1093. (doi:10.1126/science.1145803)
14. Kashiri N *et al.* 2018 An overview on principles for energy efficient robot locomotion. *Front. Robot. AI* **5**, 129. (doi:10.3389/frobt.2018.00129)
15. Ijspeert AJ. 2014 Biorobotics: using robots to emulate and investigate agile locomotion. *Science* **346**, 196–203. (doi:10.1126/science.1254486)