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EDITORIAL

Expanding knowledge of contracting muscle

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Muscle chapters in physiology textbooks tend to be short and narrowly focused; muscle has been portrayed as both genetically fixed and seemingly singular in function to produce work while shortening. However, the suite of muscle functions is extremely broad, including noise maker, thermogenic organ, isometric 'lock' and a power source for projectiles, in addition to driving locomotion. Likewise, the force that active muscles produce may be generated during shortening, lengthening or static (isometric) muscle 'contractions' (the term itself a legacy of that narrow view) to accomplish these diverse tasks. Recent molecular and biomechanical discoveries have forced a serious re-evaluation of muscle and its structural and functional complexity. Journal of Experimental Biology has been, and continues to be, a strong voice in promoting dissemination of current developments in cutting edge muscle research. This special issue is inspired by these discoveries and insights. While not intended to address all aspects of muscle structure and function, it successfully connects diverse research perspectives to tackle how recent insights have modified and expanded our understanding of skeletal muscle.

The exponential expansion of molecular research is now, really for the first time in 60 years, allowing an expansion of the sliding filament theory introduced in 1954 (Huxley and Niedergerker, 1954; Huxley and Hanson, 1954). The foundation for this special issue was thus an examination of the molecular composition of the myofibrils, beginning with the cytoskeleton and incorporating new insights on myosin, actin and the cross-bridges they form, including mechanisms of excitation–contraction coupling. How are these relationships modified when we add titin, the filament unknown to the Huxleys and their colleagues? The role of this enormous protein provokes both excitement and some controversy. While the sliding filament theory remains a very useful paradigm, it can now be modified with decades of molecular discovery, not least of which includes this still relatively mysterious giant molecule.

When muscle is activated, the force it produces is highly dependent on muscle movement. Both the magnitude of the force and the energy cost to produce that force vary greatly, depending not only on the velocity of length change but also, more importantly, on the direction of that length change. In particular, our understanding of lengthening (eccentric) contractions has lagged behind the considerable body of knowledge focusing on shortening (concentric) contractions. In addition to unravelling the mechanics of this distinction, the role of the central nervous system in the control of these contractions is only starting to be understood.

Another topic that was traditionally disregarded to some extent is the role of muscle phenotypic plasticity, in particular how muscle use impacts muscle structure. While the role of exercise training has long been recognized, only recently has the magnitude of such use–structure feedback been appreciated. Much of this work has focused on the signaling pathways within muscle and the very interesting observation that many of these may respond to single bouts of 'exercise' or repeated exercise, i.e. a single change in muscle use pattern. Another poorly understood, but intriguing, aspect of muscle plasticity is the observation of muscle memory; there are mechanisms that can permanently modify the response of muscle tissue to specific stimuli, once muscle has been subjected to these stimuli.

As the mechanical properties of muscle respond to use, so too must muscle energetics. Muscle tissue is a major energy sink, consuming 20% of an animal's resting energy requirement and up to 95% during maximal muscle work. The understanding of muscle energetics now includes consideration of the nature of the fuel used by the muscle as well as how aging impacts muscle mitochondrial function.

Of course, it is the actions of muscle (i.e. the whole-animal function) that produce the selective forces that have shaped this interesting tissue. Thus, it is the final goal of this special issue to move outside the muscle to examine muscles as machines that power locomotion. By putting muscles into this whole-animal context, it is possible to employ a systems-analysis approach. How is the functional system a product of individual muscle component parts? How do muscles partner with connective tissue in tendons and aponeuroses to form a muscle–tendon unit that is capable of storing and recovering elastic recoil potential energy? When we 'reconstruct' the muscle and place it back into the context of a running animal, what are the final insights that muscle research can yield? Finally, in keeping with the Krogh tradition of comparative physiology, we also recognize the utility of carefully selecting models for the study of these important questions. Thus, insights from bird flight, hibernation and running in birds and macropods can help develop specific exercise protocols for disease prevention and intervention.

References

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