Mechanosensation by muscle spindles during active muscle-tendon work loops

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Introduction

While mechanosensation of muscle state is crucial for motor control, our understanding of what mechanosensors encode may be deeply flawed. Classic studies of mechanosensation used passive stretching paradigms and these foundational works concluded that primary muscle spindle receptors (1a afferent nerves) encoded muscle length or velocity while Golgi tendon organs (1b afferent nerves) encoded muscle force\textsuperscript{1}. Unfortunately, these results may not accurately represent muscle-tendon functions in a freely moving animal. First, locomotive muscles are not always passive. In a passive stretch a muscle fiber and its associated elastic structure both lengthen, thus force and length are \textit{coupled} in directionality. However, active muscle fibers function with elastic structures such as tendons and aponeuroses. During an active contraction a muscle fiber is activated, it produces force and if the force is great enough, the fiber will shorten and lengthen the elastic structure. Thus, force and length are \textit{decoupled} in directionality\textsuperscript{2}. Lastly, during locomotion muscle fiber length change patterns are cyclical and emerge from the interaction of muscle-tendon forces and body dynamics\textsuperscript{3}. This perspective motivates us to revaluate the roles of mechanosensors in encoding sensory information.

Methods

We combined in situ muscle-tendon (MT) preparations with simultaneous intra-axonal recordings in female Wistar rats (IACUC #A18042; Fig. 1). We compared two dynamic protocols. 1) A \textit{passive condition} where the MT interacts with a virtual body mass that is dropped and stretches the MT until the mass position is damped. 2) An \textit{active work loop protocol} where stimulation is applied at a set frequency and the servomotor applies MT length change according to dynamics of a mass in gravity (Fig. 2).

Results and Discussion

Our long-term goal is to establish a bench top framework for re-evaluating the roles of muscle receptors in encoding sensory information during locomotion.

Figure 1: Medial gastrocnemius (MG) activated by stimulation of ventral root and instrumented with sonomicrometry crystals to measure muscle fascicle length. Instantaneous firing rate (IFR) of proprioceptors measured with intra-axonal microelectrode in the dorsal root and physiologically characterized as a muscle spindle\textsuperscript{4}.

Figure 2: Two real-world conditions with the same muscle spindle recordings. A) \textit{passive condition} where the MT damps a virtual mass and B) an \textit{active condition} where MT is stimulated at 2.6Hz. In the bottom panel, muscle fiber lengths are represented with a color line while MT length is represented with a black line.

Figure 3: Work loop dynamics observed under the two conditions with the same muscle spindle recordings. Note that for the same forces or muscle fiber lengths, the muscle spindle responds differently (size = IFR in peaks per second)

Under novel real world conditions where the muscle is active, the fiber length is decoupled from force and it interacts with a virtual body mass, we observe that a muscle spindle operates differently than it does in passive conditions. Specifically, muscle spindles respond to increases in force even when the fiber is shortening. Furthermore, these work loops demonstrate that a muscle spindle response is more complex than a simple stretch receptor.

Significance

Here, we demonstrate the feasibility of in situ experiments that employ muscle-tendon work loops\textsuperscript{2,3} in combination with direct recordings from muscle spindle receptors\textsuperscript{4}.

References