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Time course for the development of muscle history in lumbar paraspinal muscle spindles arising from changes in vertebral position

Weiqing Ge, PhD[a,b], Joel G. Pickar, DC, PhD[a,*]

[a]Palmer Center Chiropractic Research, Neurophysiology, 741 Brady Street, Davenport, IA 52803-5209, USA

[b]Department of Physical Therapy, Youngstown State University, One University Plaza, Youngstown, OH 44555, USA

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Abstract

BACKGROUND CONTEXT: In neutral spinal postures with low loading moments, the lumbar spine is not inherently stable. Small compromises in paraspinal muscle activity may affect lumbar spinal biomechanics. Proprioceptive feedback from muscle spindles is considered important for control of muscle activity. Because skeletal muscle and muscle spindles are thixotropic, their length history changes their physical properties. The present study explores a mechanism that can affect the responsiveness of paraspinal muscle spindles in the lumbar spine.

PURPOSE: This study has the following two aims: to extend our previous findings demonstrating the history-dependent effects of vertebral position on the responsiveness of lumbar paraspinal muscle spindles and to determine the time course for these effects. Based on previous studies, if a cross-bridge mechanism underlies these thixotropic effects, then the relationship between the magnitude of spindle discharge and the duration of the vertebral position will be one of exponential decay or growth.

STUDY DESIGN/SETTING: A neurophysiological study using the lumbar spine in a feline model.

METHODS: The discharge from individual muscle spindle afferents innervating lumbar paraspinal muscles in response to the duration and direction of vertebral position was obtained from teased filaments in the L_6 dorsal roots of 30 Nembutal-anesthetized cats. The L_6 vertebra was controlled using a displacement-controlled feedback motor and was held in each of three different conditioning positions for durations of 0, 0.5, 1, 1.5, and 2 seconds. Two of the conditioning positions stretched or shortened the lumbar muscles relative to an intermediate conditioning position. Conditioning positions for all cats ranged from 0.9 to 2.0 mm dorsal- and ventralward relative to the intermediate position. These magnitudes were determined based on the displacement that loaded the L_6 vertebra to 50% to 60% of the cat's body weight. Conditioning was thought to simulate a motion segment's position that might be passively maintained because of fixation, external load, a prolonged posture, or structural change. After conditioning positions that stretched (hold-long) and shortened (hold-short) the spindle, the vertebra was repositioned identically and muscle spindle discharge at rest and to movement was compared with having conditioned at the intermediate position.

RESULTS: Lumbar vertebral positions maintained for less than 2 seconds were capable of evoking different discharge rates from lumbar paraspinal muscle spindles despite the vertebra having been returned to an identical locations. Both resting spindle discharge and their responsiveness to movement were altered. Conditioning vertebral positions that stretched the spindles decreased spindle activity and positions that unloaded the spindles increased spindle activity on returning the vertebra to its identical original (intermediate) position. The magnitude of these effects increased as conditioning duration increased to 2 seconds. These effects developed with a time course following a first-order exponential reaching a maximal value after approximately 4 seconds of history. The time constant for a hold-short history was 2.6 seconds and for a hold-long history was approximately half of that at 1.1 seconds.

* Corresponding author. Palmer Center Chiropractic Research, Neurophysiology, 741 Brady Street, Davenport, IA 52803-5209, USA. Tel.: (563) 884-5219, fax: (563) 884-5227.

E-mail address: Pickar_j@palmer.edu (J.G. Pickar)

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CONCLUSIONS: Thixotropic contributions to the responsiveness of muscle spindles in the low back are caused by the rapid, spontaneous formation of stable crossbridges. These sensory alterations because of vertebral history would represent a proprioceptive input not necessarily representative of the current state of intersegmental positioning. As such, they would constitute a source of inaccurate sensory feedback. Examples are presented suggesting ways in which this novel finding may affect spinal physiology.

Keywords: Muscle spindle; Lumbar spine; Thixotropy; Proprioception; Paraspinal muscles; Muscle history

Introduction

Repositioning accuracy of the lumbar spine is affected by mechanical and clinical factors. For example, a slouched sitting posture alters an individual's ability to accurately reposition their lumbar spine [1]. Clinically, low back pain patients have less lumbar repositioning accuracy [2] and need practice to reach accuracies similar to normal subjects [3]. Altered paraspinal muscle spindles and central processing were suggested to be the cause for the less refined position sense in low back pain patients [2]. The present study explores the presence of a phenomenon in the lumbar spine that can alter proprioceptive signaling from paraspinal muscle spindles.

Skeletal muscle exhibits a rheological property termed thixotropy (reviewed in Ref. [4]). This physical property represents a time-dependent change in viscosity and can occur in polymers able to form weak, breakable bonds. At rest thixotropic materials are stable; they become less viscous when deformed by shear forces. Stiffness in extrafusal or intrafusal skeletal muscle fibers is history-dependent. It is affected by the length at which a muscle is passively held and, in the case of intrafusal fibers, by the state of gamma-motoneuron discharge [5–7]. It is thought that when muscle is held at a constant length, relatively stable actin-myosin crossbridges form spontaneously establishing themselves at the prevailing muscle length. These crossbridges exhibit slower turnover rates compared with the recycling crossbridges that form during active muscle contraction [4–6,8]. If muscle length is subsequently changed, the stuck (cross-bridged) sliding filaments are unable to slip past each other. If the muscle is shortened the sarcomeres become slack and if lengthened they become taut. For intrafusal fibers, these history-dependent effects on stiffness change the responsiveness of muscle spindle afferents. Experiments in both humans and experimental preparations demonstrate that the passive length history of limb muscles alters the resting discharge and sensitivity of these proprioceptive afferents [9] and in turn alters the amplitude of *H* and monosynaptic reflexes [10,11]. In the human cervical spine, head repositioning errors were caused by the immediately preceding history of the posterior neck muscles and were thought to arise from the thixotropic properties of muscle spindles [12].

In resting hindlimb muscle of the cat, the effects of muscle history on intrafusal fibers and spindle discharge develop within 2 to 3 seconds [13]. In the lumbar spine of the cat, we found that the immediately preceding mechanical history of a lumbar vertebra also affects paraspinal muscle spindles; both their resting discharge and responsiveness to movement are altered in a manner determined by the direction of vertebral movement [14]. Compared with holding a lumbar vertebra in an intermediate position, translating it by as little as 1.0 to 2.2 mm in a direction which stretches the muscle spindle and then holding it in that position for 2 to 8 seconds significantly decreases spindle resting discharge and responsiveness on returning the vertebra to an intermediate position. On the other hand, a similar maneuver but in a direction that shortens the muscle spindle consistently increases resting discharge and responsiveness. These effects fully develop within 2 to 4 seconds of positioning [14]. Although these history-dependent changes demonstrate the thixotropic properties of lumbar paraspinal muscle spindles, they do not clearly address the underlying mechanism because the time course for their development using positioning durations less than 2 seconds has not been yet determined.

In human leg muscle, a quantitative analysis has been used to determine whether a cross-bridge mechanism is consistent with the increase in extrafusal stiffness ascribed to muscle history [8]. The passive length-tension curve of the triceps surae muscles contains an initially steep region followed by a shoulder whose magnitude is dependent on the duration over which the muscle group was previously held at a shortened length. Hufschmidt and Schwaller [8] show that the relationship between this interval and the shoulder's magnitude is an exponential function which approaches a maximal or a saturating value. This first-order exponential is consistent with an equilibrium model where cross-bridge assembly is in a state of flux, the number of crossbridges being determined by the number which attach spontaneously and the number which detach as a result of muscle movement [8]. Maintaining a muscle at constant length shifts the equilibrium toward attachment at the prevailing length.

The aim of the present study was to extend our previous findings demonstrating the history-dependent effects of vertebral position on lumbar paraspinal muscle spindle discharge [14] and to determine the time course for these effects. Vertebral positions that shortened muscle should tighten and load the spindle, increasing resting spindle discharge on return to an intermediate position. Conversely, vertebral positions that lengthen muscle should slacken