INTRODUCTION

Muscle spindles contribute to sensorimotor control mechanisms, responding to changes in muscle length thereby supplying sensory information about joint position (Burgess and Wei 1982; Gandevia 1996; McCloskey 1978). Their proprioceptive input is used for reflex adjustments and contributes to the development of internal models and body maps for adaptive and predictive control of posture and movement (Gandevia 1996; Prochazka 1996). Substantial study has been devoted to determining the position sensitivity of muscle spindles in the limb muscles both through reduced animal models (Matthews 1972) and intraneural recordings in humans (Cordo et al. 2002; Vallbo 1974). Their sensitivity is generally $<5 \text{imp}\cdot\text{s}^{-1}\cdot\text{mm}^{-1}$ of muscle lengthening or $<1 \text{imp}\cdot\text{s}^{-1}\cdot\text{°}^{-1}$ of joint rotation (Cheney and Preston 1976; Matthews 1972). In contrast, there appears to be no data in the published scientific literature on the sensitivity of muscle spindles in lumbar paraspinal muscles, likely due in part to the technical difficulty of recording neural activity from intact paraspinal tissues (Durbaba et al. 2006; Holm et al. 2002; Pickar 1999).

We sought to better understand proprioceptive mechanisms in the lumbar spine by investigating position sensitivity of paraspinal muscle spindles. We used an in vivo acute cat preparation to determine the relationship between spindle discharge and changes in vertebral position as the L6-7 facet joint was distracted. Because muscle spindles are thought to convey limb or joint position information (Burgess and Wei 1982; Gandevia 1996; McCloskey 1978) and capsule strain is correlated with intervertebral motion (Iannuzzi 2005) in human and cat spines, we measured in-plane strain of the facet joint capsule during the vertebral actuation and related this deformation to the intervertebral flexion angle associated with the magnitude of capsule strain. We compared position and angular sensitivity of lumbar axial muscle spindles with that of appendicular muscle spindles reported in the literature.

METHODS

Preparation

Experiments were performed on 12 deeply anesthetized adult cats [3.6 ± 0.4 (SD) kg]. All cats were treated in accordance with the Guiding Principles in the Care and Use of Animals approved by the American Physiological Society. The spinal column was initially prepared for neural recordings from the dorsal roots, and for mechanical movement of the L6 vertebra using an experimental preparation previously described in detail (Ge et al. 2005; Pickar 1999). Description of the preparation, neural recordings, and mechanical stimulation are presented here in shortened form. Anesthesia was induced by delivering 5% halothane in 100% O$_2$ (5 l/min) inside a plastic induction chamber and then maintained at 3% halothane (2 l/min) through a face mask. Catheters were placed in a common carotid artery and an external jugular vein to monitor blood pressure and introduce fluids, respectively. Anesthesia was then maintained with pentobarbital sodium (Nembutal, 35 mg/kg iv) and the halothane withdrawn. Additional Nembutal (~5 mg/kg) was administered when the cat showed a withdrawal reflex to noxious pinching of the toe pad, when mean arterial pressure increased $>$120 mmHg, or when the cat exhibited a pressor response to surgical manipulation. The cat was ventilated mechanically using a Harvard Respirator (Model No. 681; Harvard Apparatus, South Natick, MA). Arterial pH, Pco$_2$, and Po$_2$ were monitored every 60–90 min using a pH/blood gas analyzer.
Mechanically secured at the L4 spinous process and iliac crests using proximal portions of the L6 dorsal roots. Paraspinal muscles originating at the L4 and L1 vertebrae remained intact. The lumbar spine was mechanically secured at the L4 spinous process and iliac crests using a Kopf spinal unit (David Kopf Instruments, Tujunga, CA). Skin margins surrounding the lumbar spine were elevated and tied to four surrounding metal rods, thus forming a pool. Paraspinal tissues were bathed in warm mineral oil (37°C) to prevent the nerves from desiccating and the electrodes from short-circuiting.

Actuating the L6 vertebra

The L6 vertebra was actuated cranialward using a displacement control system (Lever System Model No. 310; Aurora Scientific, Aurora, Ontario, Canada) interfaced to a standard laboratory computer. The system consisted of hardware to control a rotary coil motor the shaft of which was attached to a 4-in-long lever arm pointing vertically downward (Ge et al. 2005; Pickar 1999). Parallel to the lever arm, a pair of adjustable tissue forceps (152.4 mm long) were suspended from a pivot and clamped tightly at their working end (1 × 2 teeth) onto the lateral surfaces of the L6 spinous process. The motor’s lever arm was connected to the forceps via a stiff metal rod attached to the forces 84.3 mm from its pivot. Thus L6 vertebral movement was obligatorily coupled to lever arm movement and determined from lever arm movement. Although the forceps pivoted about an axis, vertebral movement was considered linear because vertebral movements (≤1.2 mm) were small relative to the circumference circumscribed by the long forceps (<0.13% of the circumference). From a reference position, 0.2, 0.4, 0.6, 0.8, and 1.2 mm displacements were applied in order and in a cephalad direction. The reference position was a vertebral position that produced no passive load on the lever arm.

L6 dorsal root recordings

The L6 dorsal root was cut close to its entrance into the spinal cord and placed on a small platform. Thin filaments from the root were teased apart using sharpened forceps under a dissecting microscope until impulse activity from a single unit with a receptive field in the low back could be identified. Activity from a putative muscle spindle in the lumbar spine was first identified by its increased discharge frequency in response to gentle compression of the lumbar paraspinal tissues or to manual movement the L6 vertebra cranialward. Only afferents the discharge of which was highest in response to probing the back muscles compared with the gluteal, hip, or leg regions were used. At the end of the experimental protocols, a variety of approaches were used to confirm that the single-unit activity was indeed from a lumbar paraspinal muscle spindle including: von Frey monofilaments (Stoelting, Wood Dale, IL) to determine that the most sensitive area was in the low back; a large sustained increase (>10 Hz) in discharge to succinylcholine injection (100–300 μg/kg ia) (Pickar 1999; Smith and Eldred 1961), and decreased discharge to a muscle twitch to confirm that neural activity was from a muscle spindle. Because the peripheral nerve to deep paraspinal muscles is short and difficult to isolate, the afferent’s response to muscle contraction was determined by direct muscle stimulation (0.1–0.4 mA, 0.05 ms) using a constant current stimulator (Grass Instrument, PSIU6, West Warwick, RI) connected to a square-wave stimulator (Grass Instrument, S88). Two needle electrodes were typically inserted into either side of the most sensitive portion of the afferent’s receptive field. Conduction velocities were not obtained because they do not reliably distinguish between primary and secondary muscle spindle afferents in the low back (Ge et al. 2005).

Strain of the L6-7 facet joint capsule (FJC)

After recording neural activity, the L6-7 FJC was then exposed through a small opening in the overlying multifidus muscle. To enable measurements of FJC strain, silicone carbide particles were sprinkled randomly on the capsule and illuminated with a fiber optic light. Vertebral displacements were repeated while optically recording at 60 Hz high resolution images of the FJC using a CMOS camera system (Motion Pro Digital Image System, Redlake MASD, San Diego, CA; Fig. 1). Post hoc, mean Eulerian plane strains of the FJC were calculated using previously described methods (Ianuzzi and Khalsa 2005; Little and Khalsa 2005). Principal strains (E1 and E2) were calculated from the plane strains; only the maximal tensile strain, E1, is reported.

Protocols

Prior to beginning the experimental displacements, the L6 vertebral motion unit (including its paraspinal tissues) was mechanically “pre-
conditioned” to minimize factors contributing to hysteresis during measurements of capsule strain and to remove the effects of prior displacement history for determining muscle spindle discharge (Ge et al. 2005). Preconditioning consisted of five cycles (1.5 mm/s) actuating the L6 vertebra cranialward to its experimental displacement and then back to the initial reference position. Subsequently, muscle spindle activity was recorded in response to vertebral displacements (see loading protocol, next paragraph). The multifidus muscle then was dissected to expose the FJC and the same displacements repeated to record FJC strain.

The loading protocol consisted of a 0.9 s control period at the reference position followed by a ramp (1.5 mm s⁻¹) to a given displacement magnitude and hold (2.5 s) and then return to the reference position at the same ramp rate. Each spindle afferent received five ramp-and-hold trials (intertrial interval = 5 min). Each trial actuated the L6 vertebra to a given displacement position (0.2, 0.4, 0.6, 0.8, and 1.2 mm from reference). Figure 1 shows a representative trial to 1.2 mm maximum displacement.

Data analysis

Muscle spindle activity was first quantified as instantaneous discharge frequency (IF) calculated as the reciprocal of the time interval between successive spikes. The data were then reduced by determining the mean IF (MIF) over the 0.9 s control period and the final 0.9 s of the hold period (between cursors 1 and 2, 3 and 4 of Fig. 1), and then the difference for each afferent was calculated (ΔMIF). Position sensitivity was defined as the slope of the linear relationship between ΔMIF and vertebral displacement (measured in imp s⁻¹ mm⁻¹).

To enable comparisons with studies where joint angle was used to determine appendicular muscle spindle sensitivity, we also calculated sensitivity in terms of the intervertebral flexion angle (IVA) between L6 and L7. IVA was estimated from FJC strain measurements because we were technically unable to instrument the preparation and measure vertebral kinematics. Strains measured in the L6-7 facet joint capsule were used as a proxy measure for IVA. Estimates of IVA were calculated from our strain measurements based on the relationship determined from previous strain and joint kine-ematics data (Ianuzzi 2005), where IVA and FJC strain were measured in six cat cadaveric lumbar spines loaded in flexion with displacements that resulted in maximum moments below the spine’s torqu e limit (Fig. 2). The relationship between IVA and FJC strain was estimated using incremental polynomial regression. The data were regressed using a 0-order fit, then higher-order terms were added, and an F-test was performed to determine whether the fit was significantly improved with the adding of orders (Glantz and Slinker 2004). Only the tensile principal strain (E1) was used because it, compared with E2 (in-plane compressive principal strain), was typically larger in magnitude and exhibited smaller variability. The identified fit was second order: y = 0.4777x - 0.0049x² R² = 0.80; where y = IVA and x = percent strain of the L6-7 facet capsule. This relationship, obtained for lumbar flexion, was applied to the present study where the L6 vertebra was actuated cranialward under the assumption that, regardless of lumbar intervertebral kinematics within the plane line of the facet joint, similar magnitudes of FJC strain would produce similar defor-mations of the muscle spindle in the paraspinous muscles crossing the facet joint. Preliminary data (Pickar et al. 2008) suggest this assumption is valid for movement of the L6 vertebra because actuation in the sagittal (dorsal-ventralward) and longitudinal (caudal-cranialward) planes evoked similar muscle spindle discharge. Angular position sensitivity was measured in imp s⁻¹°⁻¹.

A repeated-measures analysis was used; random coefficient mixed models (SAS, v 9.1, Cary, NC) were fit to estimate the population linear regression model of spindle discharge on displacement and on IVA. Unless otherwise noted values are expressed as means ± SD.
vertebra stimulated all afferents. The resting discharge of two afferents became silent by the last displacement protocol yet still responded to vertebral movement. Excluding those afferents that became silent, the average coefficient of variation for resting discharge across the five position protocols was 15.2 ± 9.0% (range: 5.4–37.2%). While not always returning to identical resting values, baseline discharge remained relatively stable across protocols within a cat.

Following carotid artery injection of succinylcholine, afferent discharge began to increase within 6.6–29.0 s (Fig. 3). In some preparations just before the discharge increased, spindle discharge briefly decreased, which was likely caused by extrafusal contraction until the depolarizing blockade was established. A second succinylcholine injection was required to activate one afferent. Discharge increased to a peak and slowly returned toward baseline. The high-frequency discharge was sustained over ≥10 s, which represented the minimum duration over which data were collected after the peak discharge occurred. Average peak discharge was 68.1 imp s⁻¹ (range 23.4–199.1 imp s⁻¹) and mean instantaneous frequency over the ensuing 10 s was 42.4 imp s⁻¹ (range: 10.3–122.5 imp s⁻¹). Inspection of each response showed that discharge was sustained and not erratic as might be expected from Golgi tendon organ afferents (Dutia and Ferrell 1980). All afferents were silenced by muscle twitch during bipolar muscle stimulation.

Linear position sensitivity

The change in mean instantaneous frequency (ΔMIF) was determined at each magnitude of L₆ vertebral displacement for each of the 12 muscle spindle afferents (Fig. 4). Average ΔMIF was 7.1 ± 5.1, 11.4 ± 5.8, 16.2 ± 6.7, 19.2 ± 7.5, and 23.4 ± 8.0 imp s⁻¹ as the L₆ vertebra was actuated 0.2, 0.4, 0.6, 0.8, and 1.2 mm, respectively. Figure 4 also shows the fitted population linear regression model. The slope of this line, i.e., the estimated linear position sensitivity, was 16.3 imp s⁻¹ mm⁻¹ [10.6, 22.05, lower, upper 95% confidence interval (CI), P < 0.0001]. This estimate is conservative because the activity of one spindle in the multifidus muscle (solid, up-side down triangles in Fig. 4), while loaded by the 0.2-mm actuation did not increase further as displacement increased.
Profile plots showing the relationship between estimated muscle lengthening and ΔMIF are shown in Fig. 5. Linear position sensitivity based on muscle length using the random coefficient mixed model was 19.5 imp·s⁻¹·mm⁻¹ [12.7, 26.2 (CI), P < 0.001], 20% greater than the sensitivity estimate based on vertebral displacement. Our consideration of linear position sensitivity in the Discussion is based on the more conservative slope using vertebral displacement rather than muscle lengthening.

Angular position sensitivity

Facet joint capsule strain generally increased across the five vertebral actuations in each preparation (Fig. 6). Infrequently strain would decrease or not change despite an increase in displacement. Similar behavior has been observed in the capsule of human cadaveric spines [e.g., see Fig. 6 in Ianuzzi et al. 2004 and their discussion of potential factors contributing to such variability]. On average facet joint capsule strains increased monotonically by 1.4 ± 0.6, 1.9 ± 0.8, 3.3 ± 2.6, 4.7 ± 3.1, and 7.8 ± 4.3% at 0.2, 0.4, 0.6, 0.8, and 1.2 mm vertebral displacements, respectively. These strains were well within the physiological range of motion for the cat spine (Ianuzzi et al. 2007) and on the lower end of the strain axis for the polynomial regression (Fig. 2).

Using the polynomial regression, we calculated IVAs from individual strains measured at each level of vertebral actuation. On average, intervertebral flexion angles increased by 0.7 ± 0.3, 0.9 ± 0.4, 1.5 ± 1.2, 2.1 ± 1.4, 3.4 ± 2.0° at 0.2, 0.4, 0.6, 0.8, and 1.2 mm, respectively. Figure 7 shows the fitted population linear regression model for spindle discharge on IVA. Estimated angular position sensitivity was 5.1 imp·s⁻¹·°⁻¹ [2.8, 7.3 (CI), P < 0.0002].

DISCUSSION

In the current study, the manner in which sensitivity was determined represents the behavior of spindles from lumbar multifidus and longissimus muscles in response to a short-duration change in position of a lumbar vertebra. Teased dorsal root filaments did not contain activity from more than one discriminable paraspinal muscle spindle afferent, and only one...
afferent was recorded per cat to obtain responses from a low back that was as biomechanically intact as possible. Therefore the lumbarparaspinous fascia compartmentalizing the paraspinal muscles was not cut until the end of the experiment when the afferent’s identity was confirmed. While the small laminectomy at L5 made it impossible to isolate and cut the L6 ventral root without injuring the spinal cord, the preparation was considered functionally de-efferented because the deep level of Nembutal anesthesia, evidenced by the need for ventilation and the absence of withdrawal reflexes, likely caused little or no γ motoneuron (Collins et al. 1995; Ge et al. 2006).

Paraspinal muscle position sensitivities measured in the present study can be compared with appendicular muscles from 13 previous studies including ankle and wrist flexors and extensors, and 2 studies of dorsal neck muscles (Table 1). When SDs and sample sizes were provided, 95% CIs were calculated for comparison with the present study. Previous studies were similar having used ramp and hold stretching and having determined positional sensitivity based on spindle responses ≥0.5 s after the ramp’s end, a duration at which spindle adaptation is considered terminated (Matthews 1972). The studies represent a range of approaches by which the muscles were actually stretched. Several conclusions are drawn from the comparisons shown in Table 1.

First, position sensitivity of primary compared with secondary muscle spindles in appendicular muscles of the cat and non-human primate are similar within each species. In addition, this similarity is evident regardless of whether linear or angular sensitivity was measured. Second, appendicular position sensitivity (both linear and angular sensitivity) is slightly higher in the cat than non-human primate. Third, lumbar paraspinal muscle spindles had greater position sensitivity than appendicular muscle spindles. Our conservative estimate for lumbar linear sensitivity was 3.8–4.8 times greater than the average linear sensitivity of 3.4 imp·s⁻¹·mm⁻¹ for primary afferents (n = 10 studies) and 4.3 imp·s⁻¹·mm⁻¹ for secondary afferents (n = 8 studies) from appendicular muscles. Similarly, lumbar angular sensitivity was ~10 times greater than the 0.5 and 0.4 imp·s⁻¹·°⁻¹ for primary (6 studies) and secondary (3 studies) appendicular afferents. From the current study, 95% CIs for both linear and angular measures of position sensitivity did not contain the point estimates of sensitivity for either primary or secondary appendicular muscle spindle afferents. Similarly the 95% CIs from all previous studies contained neither the linear nor the angular measures of position sensitivity from the current study. Thus our measurement of higher position sensitivity in spindles of lumbar axial muscles compared with appendicular muscles is not likely a chance occurrence. Fourth, from the current study the CI for angular position sensitivity in the lumbar spine contained the single value estimate obtained from the cervical spine. Additional investigations are necessary before concluding that muscle spindle sensitivity in the neck is similar to that in the low back.

Several structural aspects that could contribute to the high sensitivity of lumbar paraspinal muscle spindle include their intrafusional composition, anatomical location, and intrafusional fiber stiffness. Electrophysiological methods indicate that lumbar paraspinal muscles contain a large percentage of b₂c spindles (Durbaba et al. 2006; Pickar and Ge 2006). The b₂c composition is commonly found in tandem spindles which are more

| Type of Spindle Afferent | Rectangular Sensitivity (both linear and angular sensitivity) is slightly higher than the 0.5 and 0.4 imp·s⁻¹·°⁻¹ for primary (6 studies) and secondary (3 studies) appendicular afferents. Similarly the 95% CIs from all previous studies contained neither the linear nor the angular measures of position sensitivity from the current study. Thus our measurement of higher position sensitivity in spindles of lumbar axial muscles compared with appendicular muscles is not likely a chance occurrence. Fourth, from the current study the CI for angular position sensitivity in the lumbar spine contained the single value estimate obtained from the cervical spine. Additional investigations are necessary before concluding that muscle spindle sensitivity in the neck is similar to that in the low back.

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numerous in cervical paraspinal compared with appendicular muscles (Bakker and Richmond 1981; Price and Dutia 1989; Richmond et al. 1986). Location within a muscle can also affect spindle sensitivity. In the cat extensor digitorum longus the angle of muscle fibers at the periphery relative to the muscle’s central, long axis allows the central portion to elongate at least three times further (Meyer-Lohmann et al. 1974). Muscle spindles in the central portion discharge more than those near the aponeurotic and tendinous attachment (Meyer-Lohmann et al. 1974). In neck muscles with attachments to the cervical vertebra, the deeper, central region contains the greater majority of spindles (Richmond and Abrahams 1975; Richmond and Bakker 1982). Increased passive stiffness of the spindle’s polar region containing the contractile apparatus would increase the central bag region’s deformation and consequently, the receptive ending during muscle stretch. While multiple isoforms of heavy chain subunits for myosin are specific to intrafusal fibers (Walro and Kucera 1999), what, if any, biomechanical specialization they confer to the intrafusal fiber is not known.

**Physiological perspective**

One might anticipate that the physiological characteristics of paraspinal proprioceptive input and its central processing would be adapted to the spine’s functional requirements. Because multiple functional spinal units underlie global spinal postures (White and Panjabi 1990), should neuromuscular control allow intersegmental kinematics of any one unit to exceed its normal limit (even if global posture is normal), the potential for tissue strain and injury may be introduced (Cholewicki and McGill 1996; Wilder et al. 1988). This may be particularly true during lateral bending where the accompanying coupled motions appear most controlled by lumbar muscle activity (Little et al. 2008). High positional resolution from lumbar paraspinal muscle spindles would provide a peripheral sensory mechanism contributing to intersegmental control. Centrally, such functionality appears complemented by a neural organization that would enhance intersegmental control in the lumbar spine. Intervertebral reflexes, the afferent arm of which consists of unidentified afferents traveling in the medial branch of the posterior primary ramus and the efferent arms of which travel in medial branches at the adjacent levels, have been demonstrated in the lumbar spine (Kang et al. 2002). Spinal cord recordings reveal that spindle input from longissimus muscle produces the largest synaptic potentials at segmental longissimus motoneurons (Durbaba et al. 2007; Wada et al. 2003). The input also becomes intersegmental with collaterals diverging to the longissimus motoneuronal pool at least one or two spinal segments rostral and caudal evoking smaller synaptic potentials (Durbaba et al. 2007; Wada et al. 2003). Group Ia from the longissimus muscle may diverge less than group II spindle afferents (Wada et al. 2003). Knowing whether the position sensitivity of group Ia and group II paraspinal muscle spindles differs would be important because group II spindle input appears stronger, evoking larger synaptic potentials than group Ia (Durbaba et al. 2007) while longissimus motoneuronal excitatory postsynaptic potentials (EPSPs) evoked by segmentally related spindles are more tightly coupled to its intrinsic membrane properties than segmentally distant spindles (Wada et al. 2003).

The importance of spinal proprioception, and perhaps paraspinal muscle spindles in particular, is highlighted by evidence indicating that the functional status of these spindles and/or their reflex actions might be impaired in idiopathic low back pain. Healthy individuals can accurately reposition their lumbosacral spine, but their repositioning ability is impaired when muscle spindle discharge is increased by applying vibration to the lumbar paravertebral muscles (Brumagne et al. 1999). The correct position is consistently undershot due to the misperception of vertebral position. In individuals with a history of low back pain, lumbosacral-repositioning ability is impaired even in the absence of vibration (Brumagne et al. 2000; Newcomer et al. 2000a; but see Newcomer et al. 2000b) and, paradoxically in contrast to healthy individuals, is improved with vibration (Brumagne et al. 2000). Patients with chronic low back pain have poor postural control when challenged with unstable sitting in the absence of visual feedback (Radebold et al. 2001), and their reflex responses to sudden load is delayed, more variable, and smaller in amplitude compared with healthy individuals (Radebold et al. 2000, 2001). The higher position sensitivity of lumbar paraspinal muscle spindles may have distinctive functional implications making the spine particularly sensitive to factors that alter proprioceptive processing.

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