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## The decreased responsiveness of lumbar muscle spindles to a prior history of spinal muscle lengthening is graded with the magnitude of change in vertebral position

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### Abstract

In the lumbar spine, muscle spindle responsiveness is affected by the duration and direction of a lumbar vertebra's positional history. The purpose of the present study was to determine the relationship between changes in the magnitude of a lumbar vertebra's positional history and the responsiveness of lumbar muscle spindles to a subsequent vertebral position and subsequent vertebral movement. Neural activity from multifidus and longissimus muscle spindle afferents in deeply anesthetized cats was recorded while creating positional histories of the L<sub>6</sub> vertebra. History was induced using a displacement-controlled feedback motor. It held the L<sub>6</sub> vertebra for 4 seconds at an intermediate position (hold-intermediate at 0mm) and at 7 positions from 0.07 to 1.55mm more ventralward and dorsalward which lengthened (hold-long) and shortened (hold-short) the lumbar muscles. Following the conditioning hold positions, L<sub>6</sub> was returned to the intermediate position. Muscle spindle discharge at this position and during a lengthening movement was compared between hold-intermediate and hold-short conditionings and between hold-intermediate and hold-long conditionings. We found that regardless of conditioning magnitude, the 7 shortening magnitudes similarly increased muscle spindle responsiveness to both vertebral position and movement. In contrast, the 7 lengthening magnitudes produced a graded decrease in responsiveness to both position and movement. The decrease to position became maximal following conditioning magnitudes of ~0.75 mm. The decrease to movement did not reach a maximum even with conditioning magnitudes of ~1.55 mm. The data suggest that the fidelity of proprioceptive information from muscle spindles in the low back is influenced by small changes in the previous length history of lumbar muscles.

### Keywords

lumbar spine; muscle spindle; proprioception; thixotropy; multifidus; longissimus

### INTRODUCTION

Stability, robustness and performance are attributes of the lumbar spine as a mechanical system that depend upon of a variety of biological mechanisms [McGill et al, 2003, Reeves

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et al, 2007, Solomonow 2011]. Which mechanisms become engaged depends upon both the biomechanical behavior of the spine's passive components (connective tissue comprising the intervertebral disc, tendons, ligaments, fascia, and non-contractile elements within paraspinal muscles) and the physiological behavior of the spine's active components (paraspinal muscle's contractile capacity and neural elements that control the recruitment, timing and magnitude of this contractile capacity) [McGill et al, 2003, Panjabi 1992, Reeves et al, 2007, Solomonow 2011]. A locus of direct interface between these two components is at receptive nerve endings in peripheral tissues. Somatosensory feedback signals are initiated here when these endings respond to their local biomechanical, thermal, or chemical environments. It has been suggested that feedback signals can become corrupted when biomechanical conditions adversely affect the mechanical behavior of the spine's passive components [Reeves et al, 2007, Solomonow 2011]. For example, creep in the lumbar tissues from prolonged cyclic and static loading alters the normal activity of multifidus muscle and potentially compromises spinal stability [Solomonow et al, 2003].

The importance of mechanical conditions and sensory feedback for helping to control stability in the lumbar spine [Granata et al, 2001, Moorhouse et al, 2007, Willigenburg et al, 2010] stimulated our interest in a mechanical property of muscle spindles that can corrupt signaling from this proprioceptor. First shown in limb muscles, thixotropy is a time- or history-dependent mechanical property that alters the magnitude and timing of stretch-reflexes and creates repositioning errors [Gregory et al, 1990, Gregory et al, 1987, Gregory et al, 1988, Wood et al, 1996]. These studies have revealed that despite returning a limb to identical positions, the previous history of muscle lengthening versus shortening determines whether the spindle's parent neuron increases or decreases its discharge. Thixotropic consequences are thought to arise from non-recycling, stable cross-bridges between intrafusal actin-myosin filaments which form at the length to which the muscle has been held [Hufschmidt et al, 1987, Proske et al, 1993]. These cross-bridges are thought to stiffen the spindle's sensory regions and increase spindle output when the limb muscle has undergone a previous history of shortening [Proske et al, 1992, Proske et al, 1993]. Conversely, a previous history of limb muscle lengthening decreases spindle output by slackening and unloading the spindle's sensory region. In the lumbar spine, if small changes in vertebral position can evoke similar behavior in axial muscle spindles, then postural history in the lumbar spine could distort proprioceptive input and alter feedback control of the spine.

Systematic investigation of segmental positional history in the feline vertebral column shows that spindles in the lumbar longissimus and multifidus muscles do exhibit thixotropic behavior in a number of ways. A vertebral position that lengthens for 2 seconds or longer the paraspinal muscles relative to an intermediate position significantly decreases the discharge of muscle spindles to vertebral position, passive vertebral movement, and the velocity of that movement [Cao et al, 2010, Ge et al, 2005, Ge et al, 2008]. The magnitude of the altered responsiveness is affected by the anatomical plane in which the segmental history is established [Ge et al, 2011]. Conversely, a shortening history with similar duration increases responsiveness, but the shortening history does not affect velocity sensitivity [Cao et al, 2010] and the plane in which the shortening history occurs does not affect the magnitude of the increased responsiveness [Ge et al, 2011]. How little a change in vertebral position can occur before that spinal segment's positional history alters muscle spindle responsiveness is not known. The importance of this lies in gaining an understanding of the magnitudes to which a posture might change before corrupting sensory feedback from muscle spindles. In the present study we determined the relationship between the magnitude of a lumbar vertebra's positional history and the responsiveness of muscle spindles to vertebral position and vertebral movement in a ventralward and dorsalward direction. Shortening and lengthening histories were created by systematically positioning the L<sub>6</sub> vertebra along the

spine's posterior-anterior axis using 8 conditioning magnitudes between 0 mm and 1.55 mm relative to an intermediate position (described in material and methods section). We tested the hypothesis that as the magnitude of a vertebra's positional history increases, the signaling error from muscle spindles will continue to increase in a graded fashion.

## MATERIALS AND METHODS

Experiments were performed on 60 deeply anesthetized male cats weighing 3.89 (SD 0.33) kg on average. Because the underlying muscles had to be exposed to help characterize the afferent, only one afferent was investigated in each cat in order to keep the lower lumbar spine intact during the experimental protocols. All experiments were approved by the institutional animal care and use committee. The preparation has been described previously in detail [Ge et al, 2005, Pickar 1999] and will be presented only briefly. Deep anesthesia was maintained with Nembutal (35 mg/kg, iv). A laminectomy was performed removing the caudal half of L<sub>4</sub> and all of L<sub>5</sub> to expose proximal lengths of the L<sub>6</sub> dorsal roots (Figure 1). Single unit recordings in L<sub>6</sub> dorsal root filaments were obtained from muscle spindle afferents with receptive fields in lumbar multifidus or longissimus muscles, two local muscles of which attach directly to the lumbar vertebra [Bergmark 1989]. Paraspinal tissues of the low back innervated by the L<sub>6</sub> and L<sub>7</sub> dorsal roots remained completely intact on both the left and right side. Afferents were classified as muscle spindles based upon their increased discharge to succinylcholine (100 – 400mg/kg, iv) and decreased discharge to electrically induced muscle contraction. Mechanical thresholds were obtained using calibrated nylon monofilaments (Stoelting, Ill) applied to the center of the receptive field.

Position and movement of the L<sub>6</sub> vertebra were imposed under displacement control using a feedback motor system (model 310, Aurora Scientific Inc., Ontario, Canada). The L<sub>6</sub> spinous process was attached to the motor's drive shaft through a pair of forceps which were translated ventral or dorsalward to load and unload the muscle spindles by changing vertebral position and paraspinal muscle length. The L<sub>6</sub> vertebra was initially positioned so that paravertebral tissues exerted no net tension against the feedback motor's drive shaft. This position for the L<sub>6</sub> vertebra was termed "intermediate". The spine's orientation appeared similar to the cat's standing posture and the lumbar muscles were likely closer to their resting length than to a stretched or shortened length as previously discussed [Ge et al, 2011].

Displacement magnitudes used to create positional histories of the L<sub>6</sub> vertebra were called "conditioning magnitudes" and were calculated relative to a maximal vertebral displacement. Maximal displacement was defined as the L<sub>6</sub> vertebral displacement which loaded the vertebra with 50–60% of the cat's body weight (BW). Based upon our previous experience, a larger percentage created maximal displacements which often tore the nerve filament from the electrode. Maximal displacements were obtained prior to beginning the experimental protocols and ranged between 0.5 and 2.3mm. Eight conditioning magnitudes were tested: 0, 5, 15, 25, 35, 50, 75, or 100% of maximal displacement. The average 100% conditioning magnitude was 1.55 (SD 0.24) mm, similar to that measured and used in previous studies [Cao et al, 2010, Ge et al, 2011, Ge et al, 2005, Ge et al, 2008].

Each experimental protocol was comprised of 4 parts continuous in time as shown by the solid line in Figure 2 (see figure caption): 1) pre-conditioning, 2) hold-conditioning, 3) static test, and 4) dynamic test. Pre-conditioning created identical mechanical histories between protocols by placing the L<sub>6</sub> vertebra at the intermediate position for 5 seconds then by rapidly moving it dorsalward then ventralward (10 mm/s) and repetitively (10x) to the maximal displacement. Following preconditioning, the L<sub>6</sub> vertebra was placed and held for 4s in one of three positions: 1) at the intermediate position (hold-intermediate, conditioning

magnitude = 0%) or at a relatively ventralward or dorsalward position (conditioning magnitude = (5, 15, 25, 35, 50, 75, or 100%) which 2) shortened (hold-short) or 3) lengthened (hold-long) the attached muscles. Based upon previous work a 4 seconds hold is sufficient to maximally elicit thixotropic effects in the lumbar spine [Ge et al, 2011, Ge et al, 2005, Ge et al, 2008]. Following the hold-conditioning, the effect of this history on muscle spindle responsiveness to vertebral position and vertebral movement was determined by recording spindle discharge for 0.5 seconds at the intermediate position (static test), then while the vertebra was slowly moved to the maximal displacement (0.2 mm/s) in the direction that loaded the spindle (dynamic test). At least 5 minutes elapsed between successive protocols similar to previous studies [Ge et al, 2011].

Protocols were organized in triads based upon the 7 non-zero conditioning magnitudes. A triad (e.g. the 50% conditioning magnitude triad shown in Figure 2) consisted of consecutive presentation of a hold-long and a hold-short protocol at the same conditioning magnitude and a hold-intermediate protocol (0%). The order of the triads was randomized and the order within a triad was randomized. The potential for losing the afferent due to the large number of protocols (7 triads $\times$ 3 protocols per triad) was reduced by studying the effect of only four triads in a given muscle spindle (i.e., 12 protocols/spindle). Cat's whose spindles received the four smaller conditioning magnitudes (5, 15, 25, and 35%) formed one group (cohort A, n=30 spindle afferents) and those receiving four larger conditioning magnitudes (25, 50, 75, and 100%) formed a second group (cohort B, n=30 spindle afferents). The 25% conditioning magnitude used in both cohorts provided a means to assess similarity between the 2 cohorts.

Spindle activity was measured using an approach identical to our previous work [Cao et al, 2010, Ge et al, 2011, Ge et al, 2005, Ge et al, 2008]. It was quantified as mean instantaneous frequency for the static test (MIF, where instantaneous frequency is the reciprocal of the time intervals between consecutive action potentials) and mean frequency for the dynamic test (MF). The effects of conditioning history on muscle spindle responsiveness during the static (ST) and dynamic tests (DT) were characterized as the change in MIF and MF between hold-short and hold-intermediate ( $ST_{short}$  and  $DT_{short}$ ) and between hold-long and hold-intermediate ( $ST_{long}$  and  $DT_{long}$ ). Hence, a positive  $\Delta$  indicated an increase and conversely, a negative value indicated a reduction in muscle spindle responsiveness relative to a relatively neutral posture.

A power calculation indicated that 30 afferents provided (1 -  $\beta$ )=0.80 power at  $\alpha=0.05$  level of significance to detect a 5 imp/s difference between conditioning magnitudes. Based upon a recent study in the lumbar spine [Cao et al, 2009], a 5 imp/s difference could represent a 0.5 mm change in paraspinal muscle length. Statistical analyses for cohort A and B were conducted separately. The effects of conditioning magnitude were compared with repeated measures ANOVA using a randomized complete block design. Post-hoc pairwise comparisons were performed by the Bonferroni method when conditioning magnitude was statistically significant. Assumptions of normality and homogeneity of variance were examined using residual plots. Spindle responses are reported as means (lower, upper 95% CI) unless otherwise indicated. All other values are represented as mean (SD) unless otherwise noted. Statistical analyses were conducted using SAS (version 8, SAS Institute, Cary, NC).

## RESULTS

All afferents belonged to muscle spindles being activated by succinylcholine and silenced by bipolar muscle stimulation. Receptive fields were located in either the lumbar multifidus (n = 15) or longissimus (n = 45) muscle. The most sensitive portion of each receptive field was most often found in a deep part of the paraspinal muscle close to the L<sub>6-7</sub> facet joint.

Mechanical thresholds ranged between 0.04 and 60 gm [9.7 (19.2) gm] similar to those found previously [Ge et al, 2005]. Ventralward displacement of the L<sub>6</sub> vertebra loaded all 60 muscle spindles. Average conditioning magnitudes ranged from 0.07 to 1.55 mm. (Table 1).

## STATIC TEST

Hold-long conditioning (Figure 3, downward-going bars) significantly decreased the responsiveness of lumbar paraspinal muscle spindles during the static test in both cohorts (Cohort A:  $F_{3, 119}=28.97$ ,  $p<0.001$ ; Cohort B:  $F_{3, 119}=11.50$ ,  $p<0.001$ ). Inspection of mean  $\Delta MIF$  at the 25% conditioning magnitudes suggested they were similar in the 2 cohorts. In the smaller conditioning magnitude cohort, a priori post-hoc comparisons of contiguous conditioning magnitudes showed significantly greater decreases in mean  $\Delta ST_{long}$  between the 5% and 15%, the 15% and 25%, and the 25% and 50% conditioning magnitudes. Mean  $ST_{long}$  became stable by the 50% conditioning magnitude decreasing no further between either the 50% and 75% or the 75% and 100% conditioning magnitudes. Thus, maximal effects on static responsiveness were elicited with lengthening displacements of 0.78mm (see Table 1).

Hold-short conditioning (Figure 3, upward-going bars) significantly increased the responsiveness of lumbar paraspinal muscle spindles during the static test in cohort A ( $F_{3, 119}=8.84$ ,  $p<0.001$ ) and in cohort B ( $F_{3, 119}=3.97$ ,  $p=0.01$ ). The absolute magnitude of mean  $ST_{short}$  was smaller than that of  $ST_{long}$  at each conditioning magnitude. The response was graded only between the two smallest conditioning magnitudes becoming maximal with a shortening history of 0.20 mm (15% in Table 1).

## DYNAMIC TEST

Figure 4 shows the pattern of mean spindle responses during vertebral movement. Averages calculated over 5% increments of maximal displacement provided incremental means. Regardless of the conditioning magnitude used to establish the hold-short history, response profiles were similar (gray symbols in Figure 4) with incremental mean  $\Delta DT_{short}$  approaching 0 imp/s as vertebral movement reached 20–30% of its maximum displacement (~0.3 to 0.4mm from Table 1).

Compared with the hold-short history, the dynamic response profiles were different for the different hold-long conditioning magnitudes (black symbols in Figure 4). Incremental mean  $\Delta DT_{long}$  returned toward 0 imp/s as vertebral movement approached or exceeded its own conditioning magnitude (enlarged symbols in Figure 4). Because the spindles' thixotropic behavior was removed by stretching beyond the conditioning magnitude, calculating mean  $DT_{long}$  by averaging over the entire movement (i.e. beyond the magnitude comparable to that used for conditioning) would have underestimated the effects of lengthening histories. Therefore, mean  $\Delta DT$ s were calculated over movements from the start of the dynamic test to the % of maximal displacements that were smaller than and equal to the conditioning magnitude. Because each  $\Delta DT$  represented a mean relative to the start of the dynamic test, it represented a cumulative mean (Figure 5). A priori post-hoc comparisons were made between contiguous conditioning magnitudes at comparable movements over the course of the dynamic test. Decrements in cumulative mean  $\Delta DT_{long}$  (black symbols in Figure 5) were graded with conditioning magnitude; they were significantly greater between all magnitudes except between 25 and 35%. Increments in cumulative mean  $\Delta DT_{short}$  (gray symbols in Figure 5) caused by the shortening histories were not graded with conditioning magnitude.

## DISCUSSION

This study provides several new findings about the relationship between characteristics of the lumbar spine's biomechanical history and its consequences for proprioceptive signaling from lumbar muscle spindles. First, static postures that changed a lumbar vertebra's position by as little as 0.07 mm for as little as 4 seconds altered muscle spindle responsiveness to the segment's subsequent position and passive movement. Small lengthening histories decreased responsiveness and shortening histories increased it. Prior studies have shown that relatively large displacement histories of ~1.5mm, also elicit these effects [Cao et al, 2010, Ge et al, 2011, Ge et al, 2005, Ge et al, 2008]. Second, the decreased responsiveness to even the smallest lengthening histories was 3–5 times larger in absolute magnitude than the increased responsiveness to the shortening histories (compare response magnitudes between hold-long and hold-short in Figures 3 and 5). This contrast in responsiveness also occurs with the larger lengthening histories [Cao et al, 2010, Ge et al, 2011, Ge et al, 2005, Ge et al, 2008].

The third new finding is that the history-induced alterations in spindle signaling were graded over a wide range of lengthening histories but not shortening histories. The positional (static) responsiveness continued to decrease significantly with increasing conditioning displacements but reached a plateau when these displacement histories became greater than 0.78mm. The decreased dynamic responsiveness continued to decrease up to 1.55mm, the maximum conditioning displacement studied. Once movement occurred beyond the magnitude of the preceding history, the effects of history were substantially minimized or abolished. With shortening histories, the increased static and dynamic responsiveness did not change over most of the conditioning range. Thus our hypothesis that increasing the magnitude of a vertebra's positional history will produce continuously graded increases in the signaling error of muscle spindles was partially supported for hold-long's effect on spindle responsiveness to vertebral position and fully supported for their responsiveness to vertebral movement. Our hypothesis was not supported for any of hold-short's effects.

Previous studies show that lengthening histories have two other distinctive characteristics. A hold-long but not a hold-short history alters (diminishes) the velocity sensitivity of lumbar muscle spindles [Cao et al, 2010]. In addition, only the plane of movement in which the hold-long history occurs determines the magnitude to which lumbar muscle spindle responsiveness changes [Ge et al, 2011]. One interpretation of the latter finding is that spindles in muscles originating from different vertebral levels will be differentially affected by the particular history of the lumbar spine's position (e.g, laterally bent vs anteriorly flexed vs rotated) depending upon the orientation of the facets and their relative contribution to that position. Combined, these studies indicate that lengthening histories in the lumbar spine have the greatest consequences for modifying the responsiveness of muscle spindles in the low back.

The changes in spindle behavior shown in the present study represent inaccuracies in their proprioceptive information because, despite the L<sub>6</sub> vertebra having always been similarly repositioned at the start of every static test, spindle activity was dissimilar; it depended upon the preceding conditioning history. Thus, the incoming spindle signals did not represent the actual kinematic conditions of the vertebra, the vertebra being at the intermediate position for the static test and it being moved at constant rate from that position during the dynamic test.

The errors reflected by the magnitudes of  $\Delta ST_{\text{long}}$  and  $\Delta DT_{\text{long}}$  can be considered physiologically relevant. The spindle's ability to resolve vertebral position and movement is greater in the lumbar spine than in the periphery [Cao et al, 2009, Cao et al, 2009]. Static

and dynamic sensitivities of lumbar paraspinal muscle spindles are more than three times greater than that of appendicular muscle spindles. Based upon estimates of static sensitivity [Cao et al, 2009], the decreased responsiveness between -4 and -25 imp/s shown during the static test (Fig. 4) represents vertebral position errors of  $\sim 0.25 - 1.53\text{mm}$  and angular errors of  $\sim 0.77^\circ - 4.80^\circ$ . In humans, these magnitudes constitute a substantial portion of the normal segmental ranges of lumbar motion [Panjabi et al, 1994].

A potential limitation to generalizing these results to activities of daily living is that the substantial error we measured was identified following a passive return of the vertebra from the lengthening hold position to the intermediate position. During voluntary muscle activity the spindle can become loaded due to alpha-gamma co-activation and the effects of history minimized. For example, spindle loading using strong fusimotor stimulation abolishes the effects of lengthening histories as slack is removed from the conditioned spindle apparatus and the non-recycling crossbridges broken [Gregory et al, 1986, Proske et al, 1992, Proske et al, 1993]. Similarly, progressive increases in voluntary arm muscle contraction up to 40% maximal voluntary contraction (MVC) progressively reduces the effects of lengthening histories [Winter et al, 2005]. In the lumbar spine there are several reasons to think that over a substantial range of voluntary movement, gamma-motoneuron activity to lumbar paraspinal muscle spindles is insufficient to abolish the effects of history. First, removal of history by voluntary activity is not all-or-nothing [Winter et al, 2005]. Second, recent experiments suggest that the gamma-motoneuronal pool for proximal muscles begins to be co-activated at larger fractions of MVC compared to more distal muscles [Allen et al, 2008]. The 40% MVC which abolishes the effects of history in arm muscles [Winter et al, 2005] may not do so in the spine. Third, while there are no direct studies revealing the %MVC required for various spinal movements, some information is available with which to arrive at an estimate. Calculations (rows 3 & 4 in Table 2) using anthropomorphic strength data from the lumbar spine and reported by Chaffin [Chaffin et al, 1999] (rows 1, 2 & 3 in Table 2) suggest that lumbar paraspinal muscles may be able to support a substantially flexed posture as great as  $60^\circ$  with only 30% MVC (row 6 in Table 2). Flexed postures of  $20^\circ$  and  $40^\circ$  may require only 6% and 15% MVC, respectively. Using 40% MVC as a reference point for the magnitude of alpha-gamma coactivation required to abolish the effects of history [Winter et al, 2005], lumbar muscle spindles may not receive sufficient gamma drive to abolish the effects of history created by  $60^\circ$  or less of forward flexion. As shown in the current study, histories created by changes in vertebral position as small as 0.07mm are capable of inducing spindle signaling errors. History created by small postural changes that elongate the paraspinal muscles may impair the muscle spindle's ability to provide reflex support to maintain spinal stability during subsequent postural tasks or mechanical perturbation.

In conclusion, the present study showed that the fidelity of proprioceptive information from muscle spindles in the low back is influenced by small changes in the previous length history of lumbar muscles. We speculate that lumbar postures maintained away from neutral or mechanical factors which impair segmental stability and allow excessive vertebral movement can create signaling errors in the lengthened spinal muscle. These errors would be augmented by errors in the shortened, agonist muscle. The data suggest that performing full-range spinal motions would minimize proprioceptive errors that might arise following prolonged postures during, for example, long-distance driving, desk-sitting or industrial tasks. The effects of history may be a previously unrecognized factor contributing to motor control problems and possibly tissue injury in the low back. History may be one of the predisposing factors that determines whether spinal buckling and tissue injury occur in low load tasks [Preuss et al, 2005].

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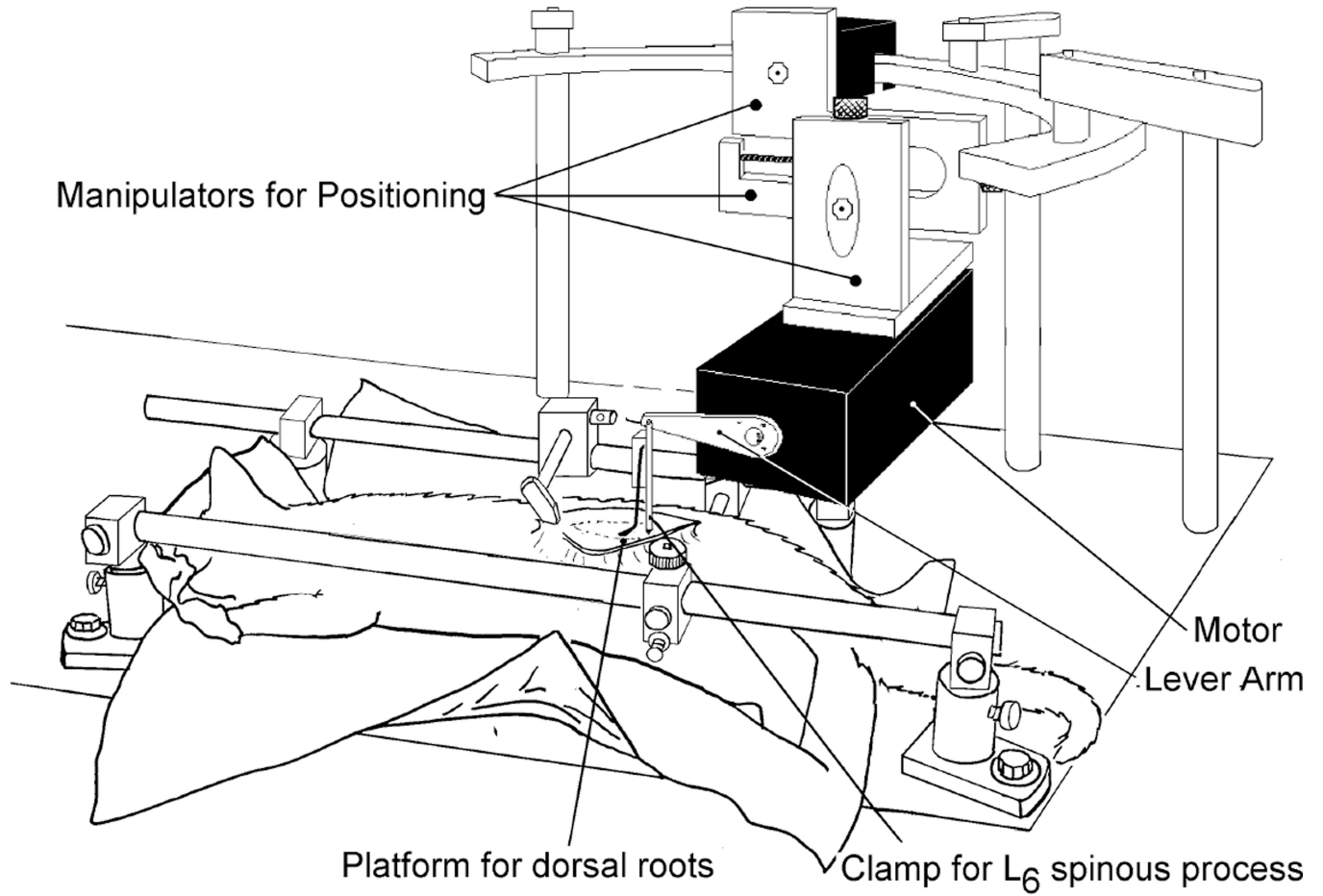
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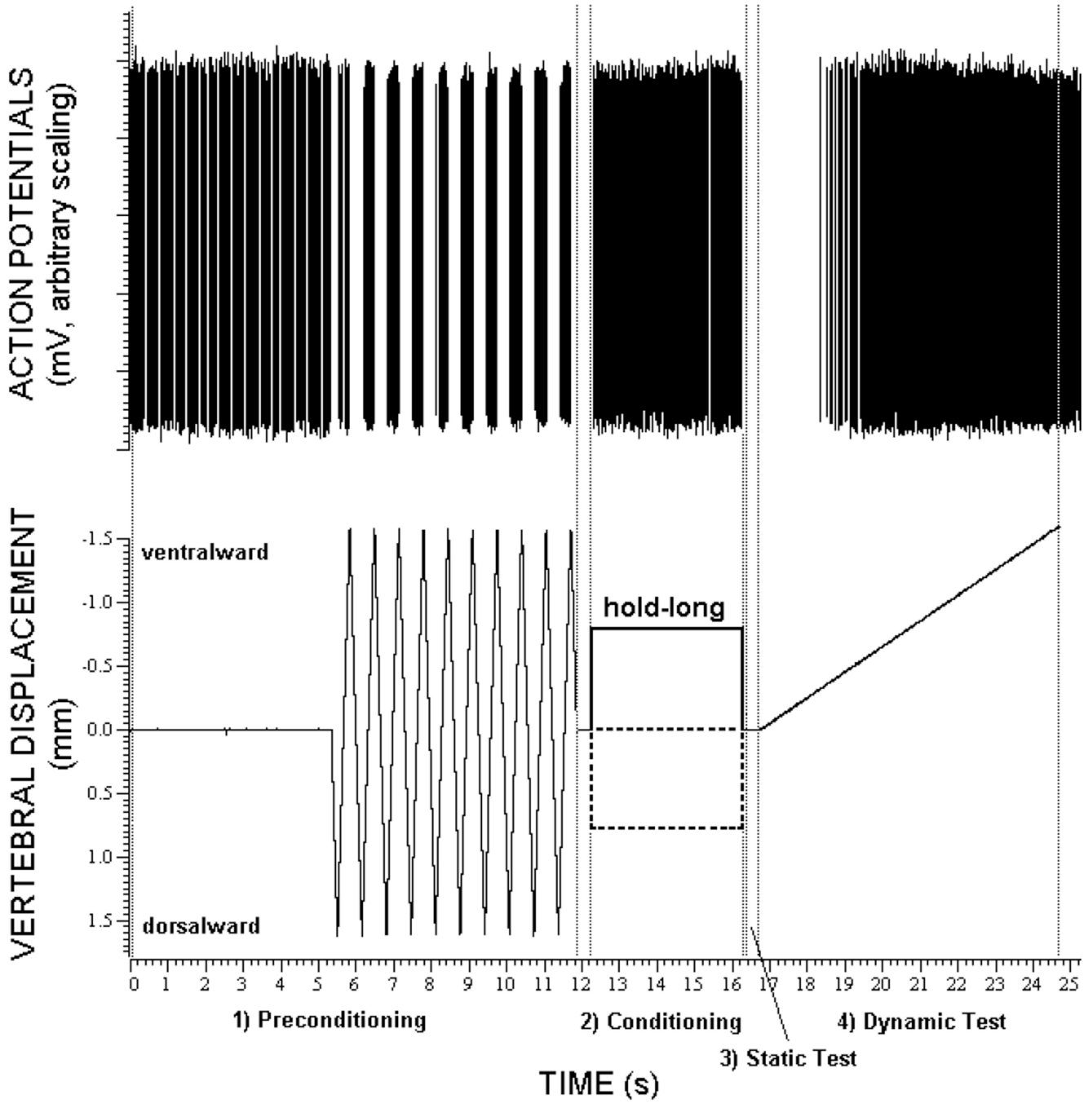
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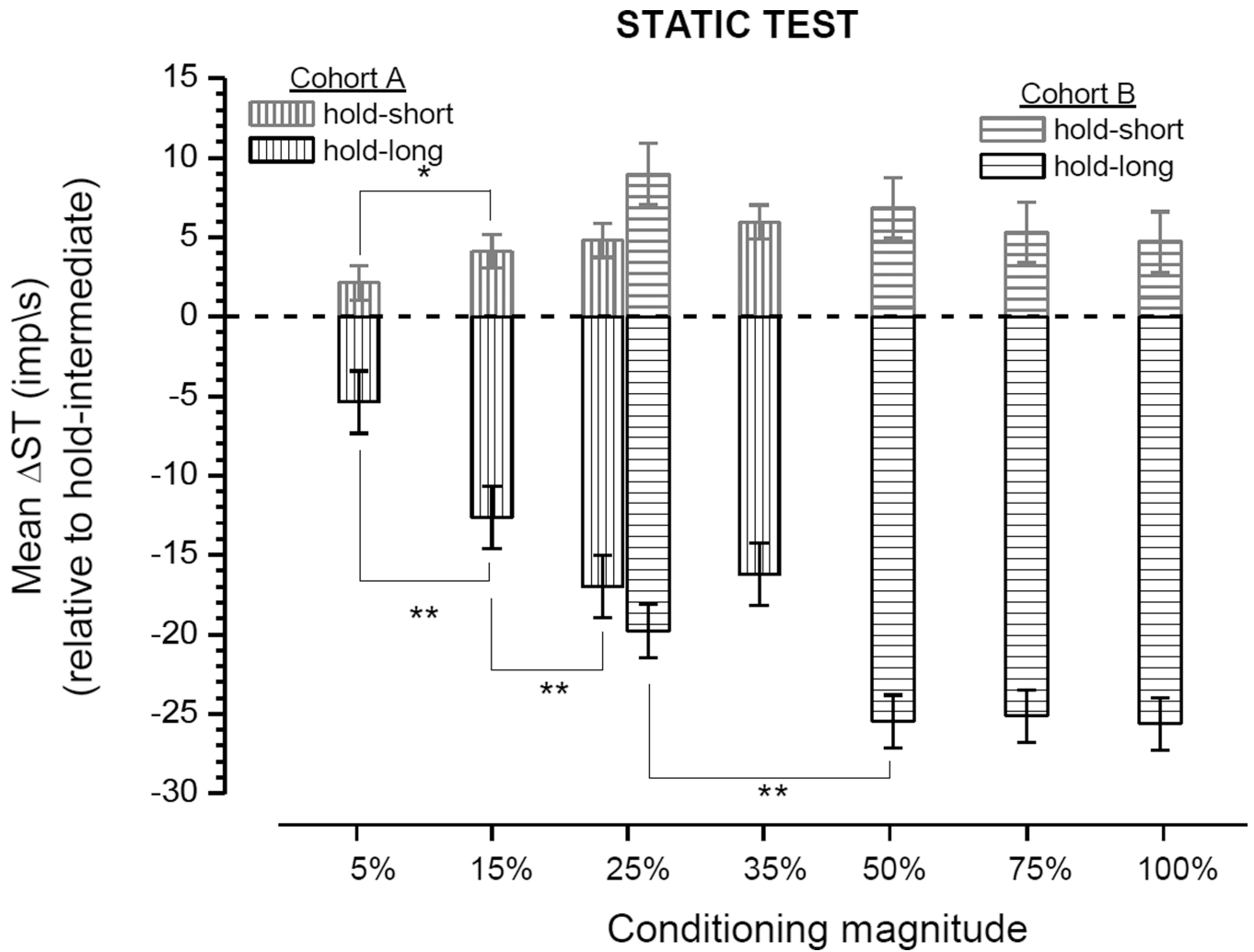
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**Figure 1.**  
Schematic of experimental setup

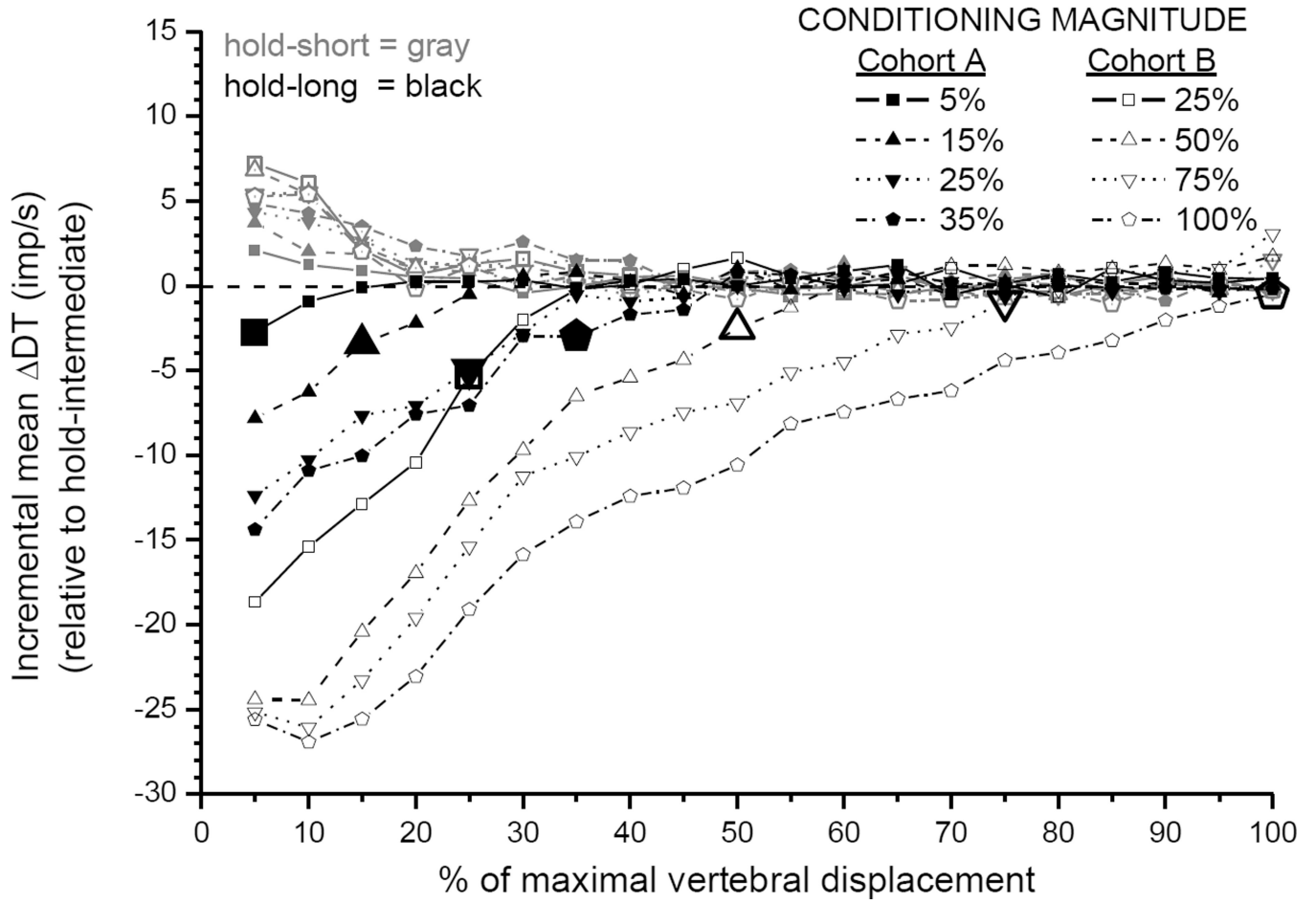


**Figure 2.** Original recording showing the mechanical testing protocol and neural activity.. Numbers below the x-axis identify the protocol's 4 parts as described in the Methods. Vertebral displacements during the hold-long protocol are depicted in the bottom panel (solid line) accompanied in the top panel by raw nerve activity from a muscle spindle afferent. Dashed lines in the bottom panel represent displacements applied during hold-intermediate and hold-short conditioning and signify the only differences in history between the protocols. 50% hold-long and hold-short conditioning magnitudes ( $\pm 0.8\text{mm}$ ) based upon a maximal displacement of 1.6mm relative to the intermediate position are shown.



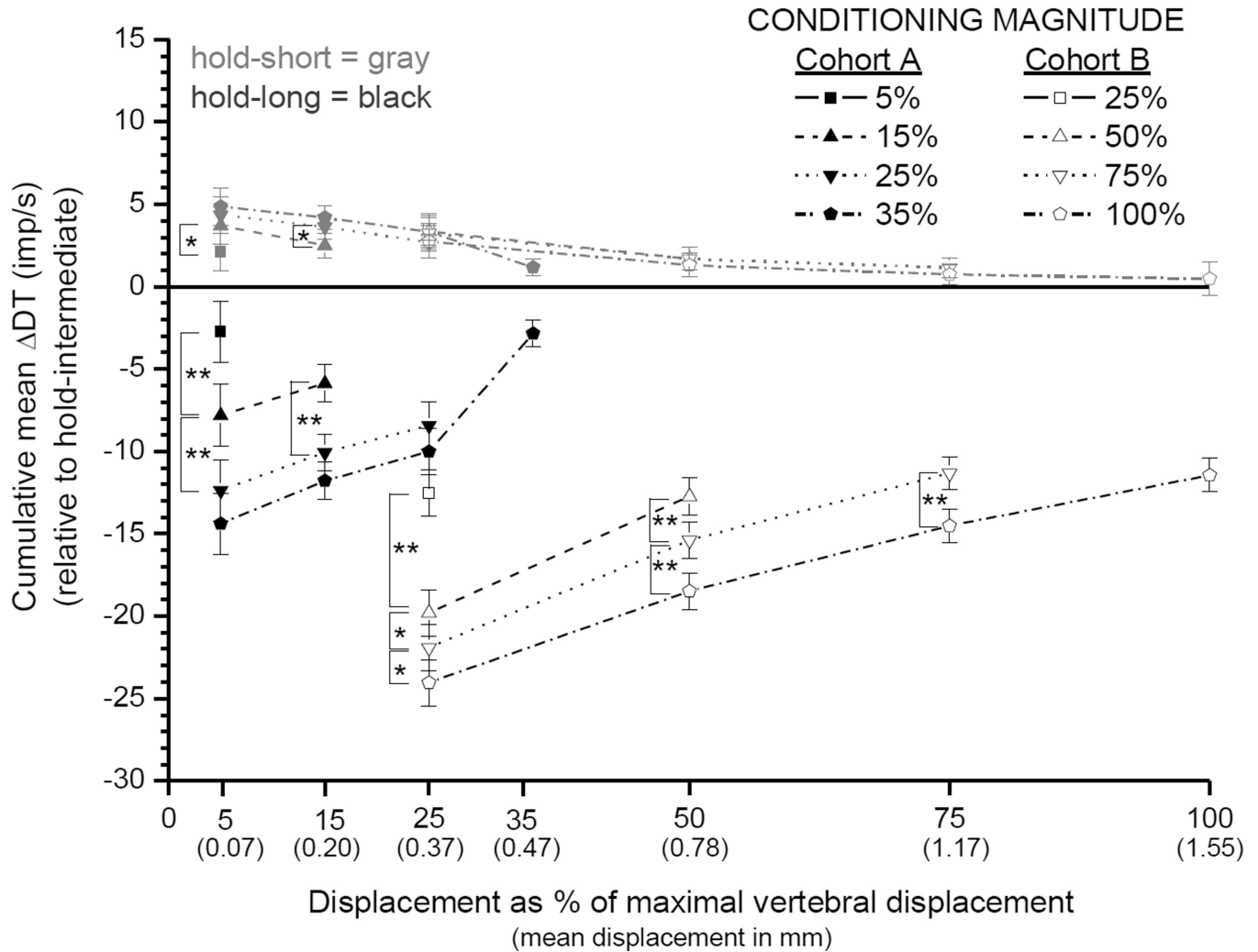
**Figure 3.** Effects of hold-long and hold-short conditioning magnitudes on mean lumbar paraspinal muscle responses during the static test. Error bars denote 95% confidence intervals. Horizontal line at 0 indicates where spindle responses were no different from the hold-intermediate conditioning history.  $\Delta$ ST, change in mean instantaneous frequency during the static test compared with hold-intermediate. \* p < 0.01 and \*\* p < 0.001 compared with next smaller conditioning magnitude. See methods for definition of maximal displacement

### DYNAMIC TEST



**Figure 4.** Effect of conditioning magnitude on muscle spindle responses over the time course of the dynamic test.  $\Delta DT$  represents the mean change during the dynamic test within successive bins representing a 5% increment in vertebral movement.

### DYNAMIC TEST



**Figure 5.** Effect of hold-long and hold-short conditioning magnitudes on mean lumbar paraspinal muscle responses during dynamic test movement. Each symbol represents a cumulative change in discharge obtained by averaging over the interval from the beginning of the dynamic test to each movement magnitude less than and equal to the conditioning magnitude used for that protocol. Error bars denote 95% confidence intervals. Horizontal line at 0 indicates where spindle responses were no different from the hold-intermediate conditioning history.  $\Delta$ DT, change in mean frequency during the dynamic test compared with hold-intermediate. \*  $p < 0.01$  and \*\*  $p < 0.001$  compared with next smaller conditioning magnitude. See methods for definition of maximal displacement.

**Table 1**

Conditioning magnitudes and the associated vertebral displacements used to create history in the 2 cohorts. Each cohort consisted of 30 afferents.

Conditioning Magnitude (relative to maximal displacement)	Actual Vertebral Displacement Mean (SD)	
	Cohort A	Cohort B
5%	0.07 (0.01)mm	-
15%	0.20 (0.04)mm	-
25%	0.34 (0.07)mm	0.39 (0.06)mm
35%	0.47 (0.09)mm	-
50%	-	0.78 (0.12)mm
75%	-	1.17 (0.18)mm
100%	-	1.55 (0.18)mm

**Table 2**

Estimated %MVC required to statically maintain the trunk at 20°, 40° and 60° forward flexion.

	Flexion Angle (FA)			Source*
	20°	40°	60°	
A. Trunk mass (including torso, head, neck, arms but not pelvis)	←	35%bm	→	Table 3.11 & Appendix B.1
B. Distance from pivot at L <sub>5</sub> -S <sub>1</sub> intervertebral disc to center of trunk mass at T <sub>8-9</sub> intervertebral disc	←	26.06cm	→	Table 3.9 & Appendix B.2
C. Calculated moment arm from L <sub>5</sub> -S <sub>1</sub> (B. *sin(FA))	8.91cm	16.75cm	22.57cm	
D. Calculated moment required to support 60kg male (A. * C. * 9.8kg m/s <sup>2</sup> )	18.34Nm	34.47Nm	46.82Nm	
E. Maximal strength for torso extension for males	288Nm	232Nm	171Nm	Table 4.5
F. Estimated %MVC required to support trunk mass (D./E.) *100%	6.3%	14.9%	27.4%	

bm, body mass; cm, centimeters, Nm, Newton-meters, MVC, maximal voluntary contraction.

\* Data obtained from tables or narrative in Chaffin et al (1999) which also provides the original source.