Vestibular control of deep and superficial lumbar muscles

Running title: Lumbar muscle regional responses to vestibular stimulation

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Abstract: 247 words

Manuscript: 6691 words

Number of figures: 6

ABSTRACT:

The active control of the lumbar musculature provides a stable platform critical for postures and goal-directed movements. Voluntary and perturbation-evoked motor commands can recruit individual lumbar muscles in a task-specific manner according to their presumed biomechanics. Here, we investigated the vestibular control of the deep and superficial lumbar musculature. Ten healthy participants were exposed to noisy electrical vestibular stimulation while balancing upright with their head facing forward, left or right to characterize the differential modulation in the vestibular-evoked lumbar extensor responses in generating multidirectional whole-body motion. We quantified the activation of the lumbar muscles on the right side using indwelling (deep multifidus, superficial multifidus, caudal longissimus (L4) and cranial longissimus (L1)) and high-density surface recordings. We characterized the vestibular-evoked responses using coherence and peak-to-peak cross-covariance amplitude between the vestibular and electromyographic signals. Participants exhibited responses in all lumbar muscles. The vestibular control of the lumbar musculature exhibited muscle-specific modulations: responses were larger in the longissimus (combined cranio-caudal) compared to the multifidus (combined deep-superficial) when participants faced forward ($p<0.001$) and right ($p=0.011$) but not when they faced left. The high-density surface recordings partly supported this observation: the location of the responses was more lateral when facing right compared to left ($p<0.001$). The vestibular control of muscle sub-regions within the longissimus or the multifidus was similar. Our

results demonstrate muscle-specific vestibular control of the lumbar muscles in response to perturbations of vestibular origin. The lack of differential activation of lumbar muscle sub-regions suggests the vestibular control of these sub-regions is co-regulated for standing balance.

Keywords: Lumbar muscles, erector spinae, vestibular system, EMG, electrical stimulation

KEY POINTS

We investigated the vestibular control of the deep and superficial lumbar extensor muscles using electrical vestibular stimuli.

Vestibular stimuli elicited preferential activation of the longissimus muscle over the multifidus muscle. We did not observe clear regional activation of lumbar muscle sub-regions in response to the vestibular stimuli.

Our findings show that the central nervous system can finely tune the vestibular control of individual lumbar muscle and suggest minimal regional variations in the activation of lumbar muscle sub-regions.

Category: Control of movement

INTRODUCTION:

The erect posture adopted by bipeds places critical mechanical requirements on the lumbar musculature for spinal stability and movement. The architecture and anatomy of the multi-layered lumbar extensor muscles result in regional differences in the force vector and resulting net vertebral moment each muscle produces, dictating their role and function in the control of upright posture and torso movements (Macintosh et al., 1986; Macintosh JE & Bogduk N, 1987; Rosatelli et al., 2008). The neural control of the lumbar extensor muscles exploits each muscle's mechanical advantage, resulting in well-tuned muscle activation (Eriksson Crommert et al., 2017; Moseley et al., 2002). For example, the vertebral insertions, length and orientation of the longissimus muscle fibers give this superficial muscle a mechanical advantage as a lateral flexor of the spine compared to the deeper and more medial multifidus muscle, which is reflected in their voluntary isometric activation patterns (Eriksson Crommert et al., 2017). Regional variations in lumbar muscle activation have also been reported: deep multifidus fibers appear to limit inter-vertebral shear motion while the more superficial multifidus layers act mainly as lumbar extensors (Macintosh et al., 1986; Macintosh & Bogduk, 1986; Moseley et al., 2002; Rosatelli et al., 2008). Similarly, localized motor unit territories within the cranial and caudal parts of the longissimus pars lumborum may exhibit preferential functional activation (Abboud et al., 2020). These studies provide evidence that distinct lumbar muscles or regions within a lumbar extensor muscle are preferentially recruited during voluntary tasks or in response to mechanical postural perturbations. However, the relative contribution of descending neural control to the preferential activation of lumbar muscles or regions within a muscle remains largely unknown.

The vestibular end-organs encode head linear and angular acceleration in space into neural signals that contribute to the maintenance of an upright posture and the control of

movement (Angelaki & Cullen, 2008; Cullen, 2012). In humans, vestibular contributions to axial and appendicular muscles can be probed using electrical currents applied to the mastoid processes. Electrical vestibular stimuli (EVS) evoke a virtual signal of head rotation mostly in roll (R. C. Fitzpatrick & Day, 2004; Schneider et al., 2002) that results in craniocentric whole-body balance responses (Forbes et al., 2016; Lund & Broberg, 1983; Pastor et al., 1993; Schneider et al., 2002). Consequently, participants exhibit medio-lateral whole-body responses to electrical vestibular stimuli when they face forward while their balance responses align with the antero-posterior direction when their head is turned over their shoulder. As electrical vestibular stimuli delivered with different head orientations elicit directional whole-body balance responses, it represents an ideal method to probe whether the vestibular control of the deep and superficial lumbar muscles exhibits differential activation between lumbar muscles or regions within a muscle to generate these multidirectional responses. Using surface recordings representing global activation of lumbar extensors, multiple authors have reported lumbar muscle responses to electrical vestibular stimuli that were larger on the side the head was turned (Ali et al., 2003; Ardic et al., 2000; Desgagnés et al., 2021; Forbes et al., 2013). Ali et al. (2003) also reported larger responses in lumbar than thoracic muscles and for surface recordings located 40-48mm lateral to midline. These latter observations led the authors to argue that the longissimus and iliocostalis were predominantly responding to descending neural inputs of vestibular origin. Although this indirect evidence suggests variations in the vestibular control of the lumbar musculature and minimal vestibular contributions to the multifidus muscles, this hypothesis remains to be tested.

The aim of this study was to characterize the vestibular control of the deep and superficial lumbar musculature. Our first objective was to assess the relative contribution of descending neural signals of vestibular origin to the preferential activation of lumbar muscles or regions within a muscle. We exposed 10 participants to electrical vestibular stimuli while we

recorded electromyography using indwelling electrodes inserted in the deep multifidus, superficial multifidus, cranial longissimus and caudal longissimus muscles. We also recorded simultaneous electromyography with a matrix of surface electrodes positioned on top of the indwelling recordings. We hypothesized that the vestibular control of the lumbar muscles would exhibit regional differences. Based on the findings by Ali et al. (2003), we expected the longissimus muscle would exhibit larger responses than the multifidus muscle and that the caudal regions of the longissimus would also exhibit larger responses than its cranial regions. As a secondary objective, we examined if the regional lumbar muscle responses to EVS identified with indwelling muscle recordings were present in the high-density surface electromyography (EMG). We hypothesized that the centroid of activation would shift toward the indwelling recordings showing the largest responses to EVS.

MATERIALS AND METHODS:

Participants and ethical approval. Ten healthy people participated in the study (3 females; age (years): 27.5±3.4; height (m):1.76±0.1; weight (kg): 69.1±7.4). Participants did not report any known neurological, vestibular, or back/lower limb musculoskeletal disorder lasting more than a week in the last year. All participants gave written informed consent before their participation in the experiment. The study was reviewed and approved by the University of British Columbia Clinical Research Ethics Board (H17-02672) and conformed to the standards set by the declaration of Helsinki, except for registration in a database.

Vestibular Stimulation protocol. We exposed participants to EVS stimuli to assess regional lumbar muscle activation to craniocentric multi-directional whole-body perturbations of vestibular origin. EVS activates both canal and otoliths as demonstrated in physiological studies involving animals. Current models of vestibular processing indicate that the net signal resulting from activation of all vestibular afferents will elicit a signal of angular head velocity (R. C. Fitzpatrick &

Day, 2004; Forbes et al., 2023) and an inference of linear acceleration depending on head orientation with respect to gravity (Khosravi-Hashemi et al., 2019). We applied noisy EVS in a binaural bipolar configuration using gel-coated (Spectra 360; Parker Laboratories, Fairfield, USA) carbon rubber electrodes (9 cm^2) secured over the mastoid processes. Applied percutaneously, noisy transmastoidal currents activate primary vestibular afferents innervating the otolith and semicircular canal end-organs (Forbes et al., 2023; Goldberg et al., 1982, 1984; Kim & Curthoys, 2004; Kwan et al., 2019). This artificial activation of the vestibular system induces a virtual signal of angular velocity around an axis pointing 17-19 degrees up from Reid's plane and a head-orientation dependent inferred signal of linear acceleration (Chen et al., 2020; R. C. Fitzpatrick & Day, 2004; Khosravi-Hashemi et al., 2019). We created the EVS signal in Matlab (R2019a, Mathworks, Inc., Natick, MA, USA) by generating a 120s random signal that was low-pass filtered at 25Hz (2nd order Butterworth filter) and scaled to a peak-to-peak amplitude of 8 mA, resulting in a root mean square (RMS) amplitude of 1.8 mA (Dakin et al., 2007). The resulting digital EVS signal was converted to analog using a multifunction data acquisition module (PXI-6289, National Instruments, Austin, TX, USA) and sent to an isolated constant current stimulator (STMISOL; Biopac, Goleta, CA). By convention, positive EVS signals corresponded to an anode right/cathode left EVS current applied to the mastoid processes, leading to whole-body balance responses towards the right ear (Dakin et al., 2007, 2010; Forbes et al., 2018).

Experimental protocol. First, we asked participants to stand upright and bend their trunk forward ~20 degrees while keeping their hands crossed on their chest. This posture was held for 10s to elicit lumbar muscle activation and normalize the amplitude of the EMG signals to this contraction. To investigate the vestibular control of the lumbar muscles during quiet stance, participants stood upright on a force plate with their arms crossed on their chest. We asked participants to keep their eyes closed to enhance the responses to EVS. Stance width was

standardized to each participant's foot length. To target the different mechanical functions of the lumbar musculature and reveal potential lumbar regional responses, we exploited the craniocentricity of whole-body balance responses induced by EVS (Lund & Broberg, 1983; Mian & Day, 2014) by asking participants to maintain their head forward or rotated 90 degrees to the left or right. These head on feet postures ensured the direction of the EVS-evoked whole-body balance occurred mainly in the medio-lateral direction when participants faced forward and in the antero-posterior direction when they faced left or right. The well-defined craniocentric responses to vestibular perturbations enabled us to test the relative contributions of lumbar muscles to these multidirectional whole-body responses. Participants were instructed to rotate their head over the trunk as much as possible, but they were allowed to rotate their trunk after a maximal head-on-trunk rotation was reached to achieve a 90 degrees head rotation with respect to their feet. On average, participants maintained a 90 degrees head rotation with respect to their feet by rotating their trunk ~23 degrees (range: 9.3 – 39.2 degrees). To maximize the magnitude of the medio-lateral and antero-posterior whole-body responses induced by EVS (Cathers et al., 2005; Reynolds, 2011), participants were also instructed to align Reid's plane ~17-19 degrees up from the horizontal (i.e., head extension) in all trials. An experimenter monitored the participant's head posture by observing the projection on a wall of a laser pointed mounted on their head with a headband. Each participant was exposed to three 120s trials, one for each head orientation, separated by at least 120s. The order of head orientations was randomized between participants. If no EMG activity was observed in the intramuscular electrodes (see below for details) after ~30s of EVS, the trial was stopped and repeated while asking the participant to lean slightly forward to recruit lumbar muscle activity.

Data collection. Given that previous studies (Ali et al., 2003; Ardic et al., 2000) have demonstrated that EVS elicits symmetrical responses in left and right lumbar muscles, and to limit the number of intramuscular insertions, muscle responses were recorded only from the

right side. It should be noted that the responses in the left lumbar muscles while facing right are expected to be comparable to those observed in the right lumbar muscles while facing left, but with opposite polarity (Ali et al., 2003; Ardic et al., 2000). Muscle responses of the deep and superficial lumbar muscles to perturbations of vestibular origin were investigated using both indwelling electrodes and high-density surface EMG (Figure 1). Custom-made intramuscular EMG electrodes consisted of a pair of insulated fine-wires (Stablohm 800A, California Fine Wire, Grover Beach, CA, USA) wounded together and threaded through a 25-gauge hypodermic needle (Becton-Dickinson, Franklin Lakes, NJ, USA). The ends of the recording electrodes (one end: 1-2 mm, the other end: 2-3 mm) were bent to form a small hook, and about 2 mm of insulation was removed from the longer wire end to favour multi-unit recordings. While participants were lying prone, ultrasonography (SonoSite Micro Maxx, Bothell, WA, USA) was used to identify the location of multifidus, longissimus, and lumbar spinous processes. To differentiate multifidus from longissimus, the ultrasound probe was placed over the spinous processes in a cranio-caudal orientation and moved laterally. Transition from multifidus to longissimus was identified as a change in orientation (~90 degrees) of the muscle fiber pennation angle. This process was repeated at each vertebral level from L1 to L4. We inserted indwelling electrodes under ultrasound guidance in the deep multifidus at L4; superficial multifidus at L4; caudal longissimus at L4 and cranial longissimus at L1 of the right side. We withdrew the needles after insertion, leaving only the electrode pair embedded in the target lumbar muscle. These specific deep and superficial lumbar muscle locations were chosen based on previous studies showing differential responses of superficial and deep multifidus to postural perturbations (Eriksson Crommert et al., 2017; Moseley et al., 2002, 2003) and differential activation of caudal and cranial longissimus during voluntary movements (Abboud et al., 2020). Indwelling electrodes in superficial multifidus, caudal longissimus and cranial longissimus were positioned about 10 mm deep from the superficial muscle fascia (depth measured from the skin: 14.3±1.4, 14.6±2.0 and 13.1±1.2 mm respectively), while deep

multifidus electrodes were placed as close to the vertebral lamina as possible (depth measured from the skin: 28.3±2.0 mm). Small variations both in the medio-lateral and cranio-caudal insertions were allowed to accommodate individual muscle anatomy and to ensure that all indwelling electrodes were positioned under the high-density EMG electrode grid. A common ground electrode was positioned over the left posterior superior iliac spine. Intramuscular bipolar EMG signals were band-pass filtered (analog filter, 10 –1,000 Hz; NL844 pre-amplifier and NL820A isolation amplifier, Digitimer, Welwyn Garden City, England) and amplified (×100–1,000) prior to being sampled at 4096 Hz using an 18-bit A/D converter (PXI-6289, National Instruments, Austin, TX, USA).

High-density surface EMG signals were collected using one grid of 64 electrodes (semi-disposable adhesive matrix; OTBioelettronica, Torino, Italy) arranged in 5 columns and 13 rows (one missing electrode, inter-electrode distance: 8 mm). The high-density surface EMG grid was placed with its long axis parallel to the spine, covering the skin over lumbar muscles approximately between the L1 and L4 spinous processes (Figure 1). The medial edge of the grid was placed approximately 5 mm from the middle of the lumbar spinous processes, identified using the ultrasound. The electrode grid was held in place using bi-adhesive foam, and conductive paste (Ten20, Weaver and Co, Aurora, CO, USA) facilitated the electrical contact between the skin and electrodes. Reference electrodes for the high-density surface EMG recordings were placed over the right posterior superior iliac spine and the sacrum. High-density surface electromyography signals were collected in monopolar mode using a 128-channel amplifier (EMG-USB; OTBioelettronica, Torino, Italy) that band-pass filtered (10 - 750 Hz), amplified (×200) and digitized the data at 4096 Hz using a 12-bit A/D converter.

To confirm the expected craniocentric balance responses evoked by EVS, we measured ground reaction forces using a force plate (OR6-7-1000; AMTI, Watertown, MA). Ground reaction forces

were amplified (×4000, MSA-6, AMTI, Watertown, MA) and sampled at 4096 Hz (LabVIEW and PXI-6289, National Instruments, Austin, TX, USA). When participants stood on the force plate F_Y represented medio-lateral ground reaction forces, whereas F_X represented anterior-posterior ground reaction forces (see Figure 2). By convention, we reported the forces acting on the body. We also quantified trunk rotation when participants turned their head left or right using a magnetic sensor placed over the xiphoid process (Trakstar, Ascension Technology. Inc., Burlington, VT, USA) sampled at 180 Hz (PXI-8196, LabVIEW, National Instruments, Austin, TX, USA). The EVS signal and a square wave signal were simultaneously collected with both the multifunction data acquisition module (PXI-6289, National Instruments, Austin, TX, USA) and the high-density surface EMG amplifier to ensure data synchronization.

Data analysis. Data analysis was performed in Matlab (R2019a, Mathworks, Inc., Natick, MA, USA) using custom-written algorithms. Given that muscle fibre action potentials recorded with indwelling electrodes contain higher frequency signals than those recorded with surface electrodes (Christensen et al., 1995), we filtered the EMG signals using different cut-off frequencies (4^{th} order dual-pass Butterworth filters: 100-1000 Hz for the indwelling recordings, and 35-500 Hz for the surface recordings). We chose the high pass cut-off frequencies to avoid stimulation artifacts in the EMG signals. Before extracting the cross-covariance between EVS and EMG signals (see below), we rectified the EMG signals as this is needed to characterize and extract low frequency oscillations in the muscle responses (Dakin et al., 2014). The rectification of the EMG signals further reduces the potential effect of the high pass filter cut-off frequency on the estimate of the muscle response to EVS and we have demonstrated previously that high-pass filter cut-offs up to 100Hz result in little variations of the muscle response to EVS (Forbes et al., 2013, 2020).

Background muscle activation. We quantified deep and superficial lumbar muscle activation during the standing trials because muscle activation is required to evoke muscle responses in

appendicular and axial muscles (Forbes et al., 2013). For each head orientation trial, we calculated the Root Mean Square (RMS) indwelling EMG activity over the 120s trial duration to quantify the background muscle activation during the task. To decrease variability in EMG amplitude estimates due to factors unrelated to muscle activation, data from each indwelling muscle recording were normalized to the RMS EMG activity from the corresponding muscle calculated during the 10s trunk flexion task.

Identification of responses to stochastic vestibular stimuli. We estimated the balance and vestibular-evoked muscle responses by computing coherence and cross-covariance between the EVS and the horizontal ground reaction forces (Mian & Day, 2009) or EMG (Dakin et al., 2014). Prior to performing the spectral analyses, all indwelling and surface EMG signals were full-wave rectified (Dakin et al., 2014). For each 120s trial, we computed the power spectra of the EVS stimulus $P_{ss}(f)$ and of the response $P_{rr}(f)$ (i.e. ground reaction forces or rectified EMG signals) as well as the stimulus-response cross spectrum $P_{sr}(f)$ using the Neurospec 2.0 Matlab code (based on (Halliday et al., 1995)). For each participant and each condition, we estimated the spectral characteristics of the EMG and force signals by performing a FFT of the data using 120 disjoint data segments of ~1s (4096 points). Coherence was computed by dividing the squared cross-spectrum ($P_{sr}(f)$) by the product of the stimulus and response power spectra ($P_{ss}(f)$ and $P_{rr}(f)$). At each frequency point, coherence values are bounded between 0 and 1 for systems with no linear relation and linear systems without noise, respectively (Pintelon & Schoukens, 2012). We derived 95% confidence limits for coherence spectra based on the number of disjoint segments to identify muscle and forces responses that were significantly different from 0. We also estimated the bandwidth of deep and superficial muscle responses (indwelling EMG) using the mean responses across subjects when coherence fell below the 95% confidence limit for a frequency range of at least 5 Hz (Forbes et al., 2020). To represent the time-domain correlation between EVS and muscle activity or ground reaction forces, we

computed cross-covariance values by taking the inverse FFT of the cross-spectrum (Halliday et al., 1995) and then normalized by the product of the vector norms of the input and output signals as described by (Dakin et al., 2010). This normalization returns coefficients of correlation between -1 and 1, therefore enabling comparisons between muscles and controls for expected fluctuations in EMG based on anatomical and physiological factors (see also analyses in 'Background muscle activation'); specifically, normalized cross-covariance minimizes potential variation in responses associated with changes in background EMG activation between conditions (Arntz et al., 2019). We determined the presence of muscle and force responses to EVS for each participant and condition by confirming that the estimated cross-covariance responses exceeded the 95% confidence limit estimated based on the number of disjoint segments (Halliday et al., 1995).

Ground reaction force responses. The horizontal ground reaction forces applied to the participants represent the net horizontal (AP and ML) acceleration of the centre of mass and consequently, the sum of all the muscle responses to the EVS stimulus. Thus, the direction of the evoked ground reaction force indicates the net direction of the whole-body balance response induced by EVS (Mian & Day, 2009; Reynolds, 2011). Based on our EVS convention and force plate coordinate system, positive cross-covariance between EVS and the ground reaction forces in the ML direction (F_y) indicated that anode right/cathode left currents induced whole-body linear acceleration towards the left (when facing forward, Figure 2) while negative cross-covariance indicated that anode right/cathode left currents induced whole-body linear acceleration towards the right. When participants turned their head to the right, positive cross-covariance estimates show that anode right/cathode left currents induced whole-body linear acceleration backwards while negative cross-covariance indicated that anode right/cathode left currents induced whole-body linear acceleration forward. Directions were opposite for cathode right/anode left currents. To confirm that distinct head-to-feet orientations induced the expected

direction in the net balance responses (i.e. medio-lateral direction when facing forward and antero-posterior direction with the head turned), we estimated the direction of the whole-body response using the methods described by (Mian & Day, 2009). Briefly, we rotated the coordinate system of the force plate in 1-degree increments and calculated the new force applied to the body (F_{ROT}) as follows:

$$F_{ROT} = F_{AP} \times \sin(\theta) + F_{ML} \times \cos(\theta)$$

where F_{ROT} represents the rotated direction of the whole-body balance response, F_{AP} represents the ground reaction force in the antero-posterior direction and F_{ML} represents the ground reaction force in the medio-lateral direction. We calculated the cross-covariance between EVS and F_{ROT} for rotations between -180 to 180 degrees (0 degrees defined as perturbation towards the left). We defined the direction of the net whole-body response to EVS as the F_{ROT} that resulted in the largest cross-covariance peak of the medium latency response (Figure 2).

Deep and superficial muscle responses. We first determined the presence of vestibular responses in the deep and superficial lumbar muscles (indwelling and surface recordings) by examining if the coherence and cross-covariance between the vestibular stimuli and EMG signals were significant. The cross-covariance estimates provide a measure of the biphasic EVS-evoked response akin to the muscle responses evoked repetition of square wave stimuli (Dakin et al., 2007). By convention, positive EVS-EMG cross-covariance indicates that positive (anode right/cathode left) EVS signals facilitate EMG activity and negative EVS signals inhibit EMG responses while negative cross-covariance indicates that positive (negative) EVS signals induced inhibitory (facilitatory) muscle responses. We also described the polarity of the biphasic muscle responses for all muscles and head orientations. Finally, we extracted the latency of these responses (indwelling and surface recordings) as the second peak of the biphasic response (medium latency response, occurring at ~100ms) because it is thought to represent the muscle response of vestibular origin (Cathers et al., 2005).

To compare the magnitude of the vestibular-evoked responses across muscles and conditions, we calculated the peak-to-peak amplitude of the biphasic cross-covariance (normalized between -1 and 1) estimated from individual participants for each indwelling EMG recording. For the high-density surface EMG recordings, we described the spatial distribution of the 64 normalized cross-covariance responses obtained (Figure 3) by identifying a cluster of channels showing cross-covariance higher than 70% of the highest cross-covariance value observed in the surface EMG recordings (Vieira et al., 2010). We expected the location (cranio-caudal and medio-lateral) of the centroid of the channels in the cluster to represent local variations in muscle activation identified in the indwelling recordings. We chose to represent spatial distribution of EMG activity using a cluster of channels showing cross-covariance higher than 70% rather than using the information from all channels because the centroid coordinates calculated using the 70% threshold are closer to the actual spatial localization of the largest response (Falla & Gallina, 2020). As the 70% threshold method has not been previously validated for spatial distribution of cross-covariance in lumbar muscles, we also performed the spatial distribution analysis by calculating the centroid based on information from all channels.

Statistics. Statistical analyses were performed using SPSS (v24, IBM). When data were not normally distributed (Shapiro-Wilk test), a logarithmic transformation was applied. Parametric (on the log-transformed data when necessary), or non-parametric tests (when the log-transformed data were still not normally distributed) were applied depending on whether the assumption of normal data distribution was met. Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test).

To confirm that different head orientations resulted in whole-body responses to EVS in distinct directions, the effect of head orientation (left, forward, right) on the direction of the ground reaction forces was assessed using a parametric ANOVA-equivalent test for circular data (Watson-Williams multi-sample test for equal means (Berens, 2009)). When significant, main

effects were decomposed using pairwise comparisons with p values corrected for the number of comparisons (Bonferroni). The direction of the response is reported as mean and standard deviation.

We compared the RMS amplitude of the normalized (to the lumbar flexion task) deep and superficial EMG signals across head orientations using a two-way repeated-measures ANOVA (Head Orientation [left, forward, right] × Muscle [deep multifidus, superficial multifidus, caudal longissimus, cranial longissimus]). When significant, main effects and interactions were decomposed using pairwise comparisons within each factor (effect of Muscle across head orientations; effect of Head Orientation across muscles) with p values Bonferroni corrected for the number of comparisons.

To determine potential differences in deep and superficial lumbar muscle responses to EVS, we compared the peak-to-peak cross-covariance estimated with intramuscular recordings using a two-way repeated-measures ANOVA (Head Orientation [left, forward, right] × Muscle [deep multifidus, superficial multifidus, caudal longissimus, cranial longissimus]). As we expected differences between muscle regions for different head orientations, we hypothesized an interaction between the Head Orientation and Muscle factors. When significant, the interaction was first decomposed with planned contrast analysis to determine differences in multifidus and longissimus activation for each Head Orientation, regardless of the muscle region considered (i.e. comparison between combined deep-superficial multifidus and cranial-caudal longissimus). Next, we further decomposed the interaction using Bonferroni-corrected pairwise comparisons to assess other potential regional differences in lumbar muscle activation to EVS.

To determine if the regional lumbar muscle responses to EVS identified with indwelling muscle recordings were present in the surface EMG recordings, we compared the location (cranio-caudal and medio-lateral location of the centroid) both for the cluster of channels showing cross-covariance higher than 70% of the highest cross-covariance value as well as for all channels.

We determined how head orientation influenced the location of the response observed on the surface recordings using separate Friedman tests on the cranio-caudal and medio-lateral centroid locations. When significant, main effects were decomposed using pairwise comparisons with p values corrected for the number of comparisons.

For all statistical comparisons, Bonferroni-corrected 95% confidence intervals (parametric statistics) or 25^{th} – 75^{th} percentiles (non-parametric statistics) are reported. Statistical significance was set at $p \leq 0.05$, and data are presented as mean and standard deviation, or median and interquartile range if not normally distributed.

RESULTS:

Balance responses to EVS. All participants exhibited clear and significant whole-body responses to the electrical stimuli (Figure 2). As expected, the direction of the EVS-evoked whole-body responses varied with head orientation (Watson-Williams circular statistics: $F(2,27)=121.069$, $p<0.001$; all pairwise comparisons: $p<0.001$; Figure 2). The net direction of the force vector acting on the body (Frot) was directed forward when facing left (mean angle: -91±29 degrees), backward when facing right (93±25 degrees) and to the right when facing forward (179±14 degrees; note: the variability estimate was obtained after adding 360 to negative angles due to the +/-180 degrees discontinuity for vectors pointing right).

Deep and superficial lumbar muscle responses to EVS. Participants maintained a background muscle activation in deep and superficial lumbar muscles for all head orientations (49.8±35.6% of the amplitude measured during a 20-degree trunk flexion). Participants exhibited minimal changes in muscle activation levels when maintaining standing balance with different head orientations (Head Orientation × Muscle interaction for the log-transformed RMS EMG; $F(6,54)=3.147$, $p=0.010$): we only observed a lower activation of the superficial multifidus

when facing forward (46.0±32.2%) compared to when facing left (62.9±41.3%; p=0.006, log-transformed CI: 0.105 - 0.541). Planned contrast between the multifidus (combined deep and superficial) and longissimus (cranial and caudal) muscles also revealed no differences in muscle activation between muscles or head orientations (multiple p>0.134), demonstrating that the overall activation of multifidus and longissimus was similar between muscles and not influenced by head orientation.

In response to the vestibular stimuli, all participants exhibited significant responses in the deep multifidus, superficial multifidus, cranial longissimus and caudal longissimus muscles. For all muscles, coherence was significant up to 15 Hz but the largest correlations occurred below 10 Hz (see Figure 4). The biphasic muscle responses evoked by EVS exhibited polarities that were dependent on the direction of the balance responses. When facing forward or right, the lumbar muscle cross-covariance responses were initially positive followed by a negative peak. When facing left, lumbar muscles exhibited an initial negative peak in cross-covariance followed by a positive response. The latency of the second peak of the biphasic lumbar muscle responses was 88±12 ms for the intramuscular recordings (Figure 4), corresponding to latencies generally attributed to the medium latency response of vestibular origin.

To determine if lumbar muscle responses to perturbations of vestibular origin showed regional modulations, we compared the peak-to-peak amplitude of the EVS-evoked muscle responses (cross-covariance, normalized between -1 and 1) when participants maintained different head orientations. Regional activation of the lumbar muscles was confirmed due to muscle-specific modulations in peak-to-peak responses elicited by EVS (Head Orientation × Muscle interaction: $F(2.447,22.024)=7.791$, $p=0.002$, Figure 5). Planned contrast between multifidus (combined deep and superficial) and longissimus (caudal and cranial) muscles revealed larger responses in longissimus than multifidus when facing forward ($F(1,9)=34.159$, $p<0.001$) and right ($F(1,9)=10.237$, $p=0.011$) but no difference between muscles was observed when participants

faced left ($F(1,9)=1.26$, $p=0.290$). We further analyzed regional activation of lumbar muscles to the craniocentric perturbations induced by EVS by comparing how the EVS-evoked responses varied between individual lumbar muscle regions as participants faced in distinct directions. Caudal longissimus exhibited larger peak-to-peak responses compared to deep ($p<0.001$, CI: 0.029 – 0.081) and superficial multifidus ($p<0.001$, CI: 0.036 – 0.090) when participants faced forward, as well as larger peak-to-peak responses compared to superficial multifidus ($p=0.021$, CI: 0.009 – 0.113) when participants faced right. Two tests approached statistical significance: deep multifidus vs cranial longissimus when participants faced forward ($p=$*0.055*, CI: -0.075 – 0.001) and deep vs superficial multifidus when they faced right ($p=$*0.062*, CI: -0.001 – 0.046). No other difference in vestibular-evoked responses between lumbar muscle regions was observed (p values>0.102).

Next, we further decomposed the interaction to characterize how head orientation (associated with direction of the whole-body response to EVS; see Figure 2) influenced the response from each muscle. To do so, we compared the peak-to-peak amplitude of the response from each muscle region across different head facing directions. In general, the peak-to-peak amplitude of the lumbar muscle responses to the vestibular stimuli was larger when participants faced right compared when they faced forward or left, but the analyses revealed muscle-specific differences. We observed larger peak-to-peak responses for both deep and superficial multifidus when participants faced right compared to when they faced forward (deep multifidus: $p=0.001$, CI: 0.027 – 0.091; superficial multifidus: $p=0.001$, CI: 0.002 – 0.069). Caudal longissimus showed larger responses while facing forward ($p=0.017$, CI: 0.013 – 0.122) and right ($p=0.003$, CI: 0.041 – 0.178) compared to left, but the difference in response amplitude did not reach statistical significance when comparing forward and right facing directions ($p=$*0.060*, CI: -0.086 – 0.002). In contrast, cranial longissimus showed larger responses while facing right compared to forward ($p=0.006$, CI: 0.020 – 0.104) and left ($p<0.001$, CI: 0.052 – 0.154), but the

difference in response did not reach statistical significance when comparing left and forward head orientations (p=*0.077*, CI: -0.086 – 0.004). No other differences in vestibular-evoked responses between head orientations were observed (p values>0.219). Overall, these results from the deep and superficial lumbar muscle recordings confirmed larger activation of the lumbar longissimus muscles compared to the multifidus in response to vestibular perturbations with modulations in the vestibular control of the lumbar musculature based on head orientation.

High-density surface EMG responses. In general, the muscle responses to the vestibular stimuli observed in the surface recordings were similar to those observed in the indwelling recordings: all participants exhibited significant biphasic responses in the surface recordings and coherence was significant up to 17 Hz with the largest correlations occurring below 10 Hz. The polarity of the biphasic muscle responses evoked by EVS also showed an initially positive peak followed by a negative peak when facing forward or right, and the opposite response polarity when facing left. The latency of the second peak of the biphasic lumbar muscle responses was 89±12 ms. Larger peak-to-peak muscle responses were also observed in the surface EMG recordings when participants faced right compared to when they faced forward (p=0.035, CI: 0.003 – 0.085) or left (p<0.001, CI: 0.052 – 0.136, Figure 6A).

To assess if differences in regional activation identified with indwelling recordings could be estimated with the high-density surface EMG recordings, we compared the location of the cluster of channels showing normalized cross-covariance responses larger than 70% of the peak response. We determined if the larger longissimus than multifidus responses observed with indwelling recordings when participants faced forward and right were reflected in the location of the activity cluster observed in the surface recordings. Head orientation influenced the medio-lateral location of the cluster of cross-covariance responses (Friedman's test: $\chi^2(2)=14.6$, p<0.001; Figure 6B), with the response being 5.2 mm (median; interquartile range:

2.6-8.8 mm) more lateral when participants faced forward compared to when they faced left ($p<0.001$). We did not observe any other difference in the medio-lateral (forward vs right: $p=0.076$; left vs right: $p=0.353$) or craniocaudal ($\chi^2(2)=1.4$, $p=0.497$) location of the high-density surface EMG responses. These results were confirmed when the analyses were performed on the centroid calculated from all channels (Friedman test on medio-lateral coordinate: $\chi^2(2)=16.2$, $p<0.001$; located more lateral when participants faced forward than left, $p=0.001$; no other significant comparisons, $p>0.131$). Similar to the observations from for intramuscular recordings, high-density surface EMG revealed that responses to vestibular perturbations in different directions resulted in preferential activation of different regions within the lumbar muscles.

DISCUSSION:

In the present study, we characterized the vestibular control of the deep and superficial lumbar musculature. Standing participants exhibited responses in all recorded deep and superficial lumbar muscles to perturbations of vestibular origin. The vestibular contributions to the deep and superficial lumbar musculature, however, were not uniform and revealed larger activation of the lumbar longissimus muscles compared to the multifidus muscles in response to electrical vestibular stimuli. We observed specific differences between the caudal longissimus and the deep/superficial multifidus activation to a vestibular stimulus when participants faced forward or right, but no differences were observed between the deep and superficial multifidus or between the caudal and cranial regions of the longissimus. We further confirmed that the regional vestibular activation of lumbar muscles observed with indwelling muscle recordings across head orientations could be partially identified in the surface EMG recordings as a lateral migration of the cluster of muscle activation when participants looked forward compared to when they looked left. Overall, our results suggest that multiple indwelling or surface EMG

recordings are necessary to characterize lumbar muscle responses to vestibular perturbations due to the spatial localization of these responses.

Despite targeting all deep and superficial lumbar muscles we recorded from, the vestibular control of the lumbar musculature exhibited regional differences resulting in larger activation of the longissimus than the multifidus muscles when participants faced forward or right. Our results support preliminary observations by (Ali et al., 2003) who showed larger lumbar muscle responses to EVS for surface EMG recordings located more laterally (e.g. 40-48mm from midline) and argued for the longissimus and iliocostalis as being the main contributors to the lumbar responses to vestibular stimuli. We emphasize, however, that our indwelling recordings clearly revealed that the deep lumbar multifidus muscles also responded to the vestibular stimuli and increased their responses for the head right orientation. These results were partially corroborated by the matrix of surface EMG recordings, which showed a more localized and laterally located cluster of muscle activity showing largest cross-covariance when participants faced forward compared to when they faced left. Our results show that multiple indwelling and high-density surface EMG recordings provide distinct and complementary information to characterize the vestibular control of the lumbar muscles across different head orientations. While the general responses to vestibular stimulation followed a similar distribution in the indwelling and in the high-density surface EMG, our results suggest that indwelling recordings are more suited to provide information about specific regional activation of the lumbar muscles (e.g., smaller multifidus response to EVS compared to cranial longissimus), whereas high-density electromyography may provide a global assessment of the distribution in muscle activity between conditions (e.g., shift in cluster location across head orientations). Overall, the differential modulation of EVS-evoked lumbar muscle responses based on head rotation support the hypothesis of regional organization of the vestibular control of the lumbar musculature.

In both indwelling and surface EMG recordings, we observed larger activation of the right lumbar muscles when participants turned their head to the right. These observations confirm the results from bipolar surface recordings of the erector spinae reported in other studies (Ali et al., 2003; Ardic et al., 2000). In addition, the relative muscle activation to EVS based on head posture revealed that the deep and superficial multifidus muscles exhibited similar low-level activation when participants faced left and forward whereas the longissimus muscles showed a more graded response from head left, to head forward to head right orientations. These distinctions in the relative vestibular control of the lumbar muscles may reflect the neuromechanical advantage of each muscle to generate whole-body responses to perturbations of vestibular origin. Indeed, multiple authors have argued that a muscle's response to EVS is determined by the alignment of its mechanical line of action with the direction of the perturbation induced by the virtual vestibular error signals (Britton et al., 1993; R. Fitzpatrick et al., 1994; Forbes et al., 2016). As vestibular stimuli induced virtual vestibular error signals in the frontal plane when participants faced forward, the larger responses in the longissimus compared to the multifidus could reflect its mechanical advantage to generate lumbar torque in the frontal plane given that the longissimus has a larger moment arm in the medio-lateral direction compared to multifidus. According to its main muscle fibers orientation and axial moment arm, the responses in multifidus only increased for the head right orientation, i.e. contributing to antero-posterior whole-body responses. We note, however, that vestibular-evoked responses remained larger in the longissimus while facing right, also supporting its mechanical advantage over multifidus to generate lumbar torque in the sagittal plane. This mechanical hypothesis, however, does not explain all our results. Because of the anterior-posterior direction of perturbation, we would have expected larger responses for the head left than the head forward orientation for both the longissimus and multifidus muscles. Here, the most cautious explanation relates to a down regulation of the vestibular projections to the right lumbar muscles when participants faced left. It has been well established that the vestibular

control to the right lower leg muscles exhibits a head orientation dependent modulation, i.e. a down regulation when participants face to the right (Britton et al., 1993; Watson & Colebatch, 1998). The physiological mechanisms underlying such opposite modulation of the vestibular control of the right lumbar (down regulation) and right lower leg (up regulation) muscles remains to be tested experimentally. Similarly, future work is needed to characterize the precise neural pathways underlying EVS-evoked lumbar muscle responses. For appendicular muscles, previous authors have proposed that responses evoked by EVS may involve brainstem structures (likely vestibulo- and reticulo-spinal tracts; (Britton et al., 1993; Cathers et al., 2005)), although additional integration of vestibular information may be required to initiate flexible balance-correcting responses. For example, some authors have proposed that vestibular-evoked responses to electrical stimuli may be modulated by cortical (via cortico-fugal pathways; (Marsden et al., 2005)) or cerebellar (Lam et al., 2016, 2017) structures.

In the present experiment, we did not observe differences in muscle activation between the cranio-caudal regions of the lumbar longissimus or the deep/superficial regions of the lumbar multifidus. While we did not identify differences between the cranial and caudal regions of the lumbar longissimus, only the caudal longissimus exhibited larger vestibular-evoked responses compared to both multifidus locations when facing forward and the superficial multifidus when facing right. These results do not indicate independent responses of the two regions within the longissimus evoked by the vestibular stimuli, they rather suggest similar activation patterns between the cranial and caudal regions (see Figures 4 and 5) and potentially reflect the large variability in the observed responses. Our results further suggest that although localized motor unit territories exist in the cranial and caudal regions of the lumbar longissimus (Abboud et al., 2020), potential differences in the modulation of the vestibular control of these muscle sub-regions are subtle in the tasks reported here. Indeed, Ali et al.(Ali et al., 2003) only reported differences in the cranio-caudal activation of the axial extensor muscles when

comparing EVS-evoked responses between the thoracic (T3 and T7) and lumbar (L3-L4) levels. Regarding the multifidus muscles, one may have expected that the superficial multifidus could be more effective at responding to vestibular perturbations in the antero-posterior plane: its longer and more superficial fibers makes it a more likely back extensor muscle compared to short and deep fibers of the deep multifidus that give it a primary role as a vertebral stabilizer (Moseley et al., 2002; Rosatelli et al., 2008). The lack of difference between responses to EVS for the deep and superficial multifidus, however, was expected because of the unpredictability of our vestibular stimuli. Indeed, unpredictable perturbations result in simultaneous activation of regions within the multifidus (Moseley et al., 2003). In addition, it is possible that the lumbar extension torque in response to perturbations of vestibular origin required mechanical coupling with muscle actions generating lumbar intervertebral stabilization. Hence, the question regarding whether the vestibular control of the lumbar musculature can target independently the deep and superficial multifidus muscles (such as cortical regions; (Tsao et al., 2011)) or not (such as proposed for spinal reflexes by Moseley and colleagues (Moseley et al., 2003)) remains open and requires future carefully designed experiments.

The present study has some limitations that warrant discussion. First, given the invasive nature of the study, we recruited only 10 participants. While our sample size is in line with other studies involving multiple intramuscular recordings (Héroux et al., 2015; Vieira et al., 2011), the low number of participants may have limited the identification of subtle differences in the vestibular control of lumbar muscles (e.g. activation differences between regions within a muscle). Also, we only performed recordings of the multifidus muscles at the L4 vertebral level to enable HDsEMG recordings and limit the number of indwelling recordings to minimize participants discomfort while standing upright. It is currently unclear how the cranial regions of the lumbar multifidus respond to vestibular stimuli. The EVS used in this study activates all afferents from both canal and otolith end-organs (Kwan et al., 2019), therefore the lumbar

responses described in this study may not be representative of real-life situations where the canal or otolith afferents may be activated independently. Finally, the small trunk rotation (~23 degrees) necessary for participants to maintain a 90-degree head to feet orientation may have changed the direction of force produced by the longissimus and/or multifidus between head orientations.

CONCLUSIONS:

Both indwelling and high-density electromyographic recordings yielded results indicative of larger responses of the lumbar longissimus than lumbar multifidus to perturbations of vestibular origin in the frontal plane, supporting the notion that preferential vestibular control is observed for muscles contributing to maintaining the torso upright. The similar responses observed for the deep and superficial multifidus, and for the cranial and caudal longissimus, suggest co-regulation of the vestibular control of regional lumbar muscle activation during standing balance. Our findings show that the vestibular control of individual lumbar muscles is finely tuned to enable corrective multidirectional postural reactions to perturbations of vestibular origin.

COMPETING INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

AG, JA and JSB conceptualized the study and defined the experimental protocol. AG and JA collected the data. AG analysed the data. AG, JA and JSB interpreted the data. AG wrote the manuscript. AG, JA and JSB revised and approved the final manuscript.

FUNDING RECEIVED

NSERC Discovery grant (JSB): RGPIN-2020-05438; NSERC post-doctoral fellowship (JA): PDF-516862-2018.

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Figure Legends

Figure 1*: A) Experimental set-up, depicting the position of the intramuscular EMG and high-density surface EMG recordings. B) Examples of EVS signal (top), intramuscular EMG recordings and high-density EMG recordings (HDsEMG, bottom). DM: deep multifidus; SM: superficial multifidus; CaL: caudal longissimus; CrL: cranial longissimus.*

Figure 2*: A) Drawing of the participants' head orientation on the force plate when facing left, forward and right, view from above. Grey lines identify the direction of the whole-body responses evoked by EVS for individual participants, the black line identifies the direction of the response averaged across participants. B) Individual and averaged cross-covariance between the electrical vestibular stimulation signal (EVS) and the medio-lateral or anterior-posterior forces applied to the body. Individual (grey) and average (black) direction of the force responses, calculated according to* (Mian & Day, 2009)*. N=10 participants.*

Figure 3*: A) Example of cross-covariance estimates (normalized between -1 and 1) for different channels of the high-density surface EMG (HDsEMG) while facing left for a representative participant. Grey circles identify the positive and negative peaks used to calculate the peak-to-peak responses for further analyses. B) Distributions of normalized cross-covariance responses between EVS and HDsEMG channels while facing left, forward and right. Shades of grey identify different cross-covariance values. Circles identify the channels with cross-covariance higher than 70% of the peak, and the cross markers represent the centroid of the distribution. The different spatial location of the centroid indicates different localization of the lumbar muscle response to EVS.*

Figure 4*: Cross-covariance (Xcov) and coherence (Coh, insets) between EVS and lumbar muscle activity across participants for different intramuscular recordings (rows) and head orientations (columns). Black lines identify the average response from all participants and grey lines identify individual participant responses. DM: Deep Multifidus. SM: Superficial Multifidus. CaL: Caudal Longissimus. CrL: Cranial Longissimus. N=10 participants.*

Figure 5*: Peak-to-peak cross-covariance values (normalized between -1 and 1) measured with intramuscular EMG (iEMG) when EVS was applied to participants maintaining standing balance with different head orientations. Boxplots depict median, quartiles and range, and grey circles identify responses from individual participants. Note: Here, cross-covariance values are represented as peak-to-peak calculated between the medium and early latency responses. The medium latency response was negative when participants faced left and positive when they faced forward and right. Statistical significance is only indicated for the comparisons between individual muscle regions within each direction of perturbation; readers are referred to the text for the other statistical comparisons. DM: Deep Multifidus. SM: Superficial Multifidus. CaL: Caudal Longissimus. CrL: Cranial Longissimus. * p < 0.05. *** p < 0.001. N=10 participants.*

Figure 6*: A) Peak-to-peak cross-covariance values (normalized between -1 and 1) measured with high-density surface EMG (HDsEMG) when EVS was applied to participants maintaining standing balance with different head orientations. Boxplots depict median, quartiles and range, and grey symbols identify individual participants. B) Centroid location (median and quartiles) of channels showing cross-covariance values between EVS and high-density surface EMG signals higher than 70% of the peak. * p < 0.05. *** p < 0.001. N=10 participants.*