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PRECISE CODING OF ANKLE ANGLE AND VELOCITY BY HUMAN CALF MUSCLE SPINDLES

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Abstract—Human standing balance control requires the integration of sensory feedback to produce anticipatory, stabilizing ankle torques. However, the ability of human triceps surae muscle spindles to provide reliable sensory feedback regarding the small, slow ankle movements that occur during upright standing has recently come under question. We performed microneurography to directly record axon potentials from single muscle spindle afferents in the human triceps surae during servo-controlled movement of the ankle joint. To simulate movements of the ankle while standing, we delivered random 90-s dorsiflexion/plantar flexion oscillations of the ankle joint, with a peak-to-peak amplitude of 0.7° and frequency content below 0.5 Hz. In roughly half of the trials (46%), participants held a low-level, near-isometric contraction of the triceps surae muscles. We demonstrate that afferent activity in a population of muscle spindles closely reflects ankle movements at frequencies and amplitudes characteristic of human standing. Four out of five soleus spindles, and three out of seven gastrocnemius spindles coded for at least a single frequency component of anteroposterior ankle rotation. Concatenating within muscles, coherence was significantly greater for soleus spindles at all stimulus frequencies. Voluntary contraction of the parent muscle reduced spindle sensitivity, but only significantly near the mean power frequency of the stimulus (~0.3 Hz). In conclusion, these results provide direct evidence that triceps surae muscle spindles are potentially capable of providing important sensory feedback for the control of human standing balance.

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Abbreviations: DoC, difference of coherence; EMG, electromyography.

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INTRODUCTION

Human standing is inherently unstable, with gravity generating destabilizing torques on the body. Though passive ankle stiffness from tissue deformation can account for a portion of the stabilizing torque required for balance control, it cannot on its own counteract this gravitational toppling torque (Morasso and Sanguinetti, 2002; Loram and Lakie, 2002). Consequently, active control of lower limb muscles is required to maintain upright standing balance. This active control relies on multisensory integration of afferent signals, presumably including those from muscle spindles located in the lower-limbs, which are traditionally thought to provide critical feedback regarding ankle movement (Goodwin et al., 1972; Hall and McCloskey, 1983). The human triceps surae has a high density of muscle spindle afferents, with the soleus containing ~400 spindles (0.94 spindles/g), and both heads of the gastrocnemii together containing ~150 spindles (0.4 spindles/g)(Voss, 1971; Banks, 2006). Given that the distribution of sensory receptors seems to have evolved to confer a functional advantage (e.g., cutaneous receptors are more densely packed in the fingertips; Johansson and Vallbo, 1979), the higher density of muscle spindles might indicate something important about coding the kinematic state of the soleus relative to the gastrocnemii. The soleus is the most habitually active muscle during standing (Joseph and Nightingale, 1952; Monster et al., 1978; Héroux et al., 2014), which may necessitate a high-level of sensitivity and dense populations of spindles to code for the small, slow ankle movements of standing. Additionally, the soleus is a monoarticular muscle, whose fascicle length changes depend only on ankle joint angle, while the gastrocnemii are biarticular, meaning fascicle length changes are a result of both ankle and knee joint angle (Herbert et al., 2002; Sturnieks et al., 2007). Based on this, we predict that soleus muscle spindles should provide higher fidelity information regarding physiologically relevant ankle angle movements than those of the gastrocnemii.

Owing to Achilles tendon compliance, recent indirect observations using ultrasonography of muscle fascicles during standing indicate plantar flexor tissue deformation is paradoxical in nature (i.e., soleus shortens when we lean forward), and is too small for muscles to accurately encode ankle angle (Loram et al.,

2004, 2008). Thus, the firing patterns of triceps surae muscle spindles should poorly (even negatively) correlate with ankle angle (Loram et al., 2004, 2008). In addition, the active or passive state could potentially alter muscle spindle coding properties (e.g., by altering muscle length/stiffness or fusimotor drive to the spindles), and is important to consider. α-motoneuron activity will alter the mechanics of the muscle (Maganaris et al., 1998), likely reducing the mechanical deformation resulting from small, slow ankle movements; γ-motoneuron activity, on the other hand is traditionally thought to alter muscle spindle sensitivity by modulating intrafusal fiber tension. It remains unclear whether lower-limb muscle spindle afferents code faithfully for small, low frequency ankle movements within a complex mechanical environment that includes varying kinematic states of the parent muscle and tendon stiffness, as well as activation of α- and γ-motoneurons.

As a first step, we sought to establish whether human muscle spindles residing in the triceps surae are sensitive enough to provide useful feedback regarding ankle movements within the physiological range of upright standing. Firstly, we hypothesized that the distribution of human triceps surae muscle spindles reflects the fact that – possibly as a result of its monoarticular nature – soleus muscle spindles provide the most precise code, which could possibly explain why this muscle has greater muscle spindle density than the gastrocnemius muscles (Voss, 1971; Banks, 2006). We further compared muscle spindle afferent coding properties in a passive muscle to those in an active muscle. Because the parent muscle contraction in this case places the muscle spindle under the influence of inputs that are decoupled to the ankle movement (α- and γ-motoneuron drive), we hypothesized that the correlation between firing activity and ankle movement would be reduced.

EXPERIMENTAL PROCEDURES

Participants

Nine healthy subjects (six male, three female) between the ages of 21 and 55 yr (mean 31 yr, SD 10.1 yr) with no known history of neurological disease or injury participated in this study. The experimental protocol was explained to each subject, and their written, informed consent was obtained. All procedures conformed to the standards of the Declaration of Helsinki and were approved by the University of British Columbia's clinical research ethics board.

Muscle spindle sample

We recorded from twelve muscle spindle afferents (28 trials), five from the Soleus (Sol; 11 trials), two from the Medial Gastrocnemius (MGas; eight trials), and five from the Lateral Gastrocnemius (LGas; nine trials). Given the relatively low number of units collected from MGas, we decided to collapse over LGas and MGas (Gas) for statistical comparison against Sol. Afferent origin was determined by palpation of the muscle bellies of triceps surae and the Achilles tendon, as well as by passive manual ankle rotation and active plantar flexion (Edin and Vallbo, 1990a, 1990b). Our primary test for identifying muscle spindles was to have the participant make a voluntary contraction, which led to an initial reduction/cessation of spindle firing, and then a return to baseline; we then had the participant abruptly relax, which causes an "OFF" discharge in muscle spindles. This end-of-contraction burst of firing activity is unique to muscle spindles. Alpha motor neurons and Golgi tendon organs could easily be distinguished by their behaviour at the end of contractions (firing stops). Skin stretch receptors were ruled out by manually shifting the skin overtop the receptive field, and palpating to ensure that the muscle-based receptive field remained in place. Muscle spindles were not formally classified as either primary or secondary endings in the present experiment. We obtained at least one complete 90-s trial from each afferent prior to termination of the recording due to electrode displacement.

Experimental setup

Subjects lay prone on an adjustable bed, with both legs extended and the test limb stabilized on a support (Versa Form™ Pillow, Sammons Preston Inc., Trenton, ON, Canada) (Fig. 1A). A surface-stimulating electrode was then placed on the posterior aspect of the knee at the level of the popliteal fossa to locate the approximate position of the underlying tibial nerve. A Grass S48 Stimulator (Grass Instruments, Astro-Med Inc., West Warwick, RI, USA) delivered electrical pulses (1 ms duration) at a rate of 0.5 Hz through a PSIU6 photoelectric stimulus isolation unit (Grass Instruments, Astro-Med Inc., West Warwick, RI, USA). The twitch response of the triceps surae muscle group (elicited between 30 and 90 V) and the parasthetic sensation described by the subject were used to assess the location of the nerve. We additionally used ultrasonography (MicroMaxx® Ultrasound System, SonoSite, Bothell, WA, USA) of the popliteal fossa to confirm nerve position. The skin at the popliteal fossa was cleaned with a 70% isopropyl alcohol solution before electrode insertion. A sterile reference electrode (0.2 mm diameter, 47 mm length, standard profile tip, Fred Haer Inc., Bowdoin, ME, USA) was manually inserted into the popliteal fossa ~1 cm adjacent to the predefined nerve location. A sterile recording microelectrode (0.2 mm diameter, 47 mm length, standard profile tip, Fred Haer Inc.) was then inserted at the predefined nerve location. To locate the nerve subcutaneously we relied on the visual neurogram, auditory feedback from the recording electrode (AM10 Audio Monitor, Grass Instruments, Astro-Med Inc., West Warwick, RI, USA), and at times, verbal reports of the participant. When the recording electrode was nearing the nerve, the subject reported either parasthesic sensation down the posterior side of their leg and into the foot sole, or a dull cramping of the plantar flexors. Once the recording electrode penetrated the nerve fascicle, there was a highly characteristic "spray" of neural activity heard over the audio monitor, which was

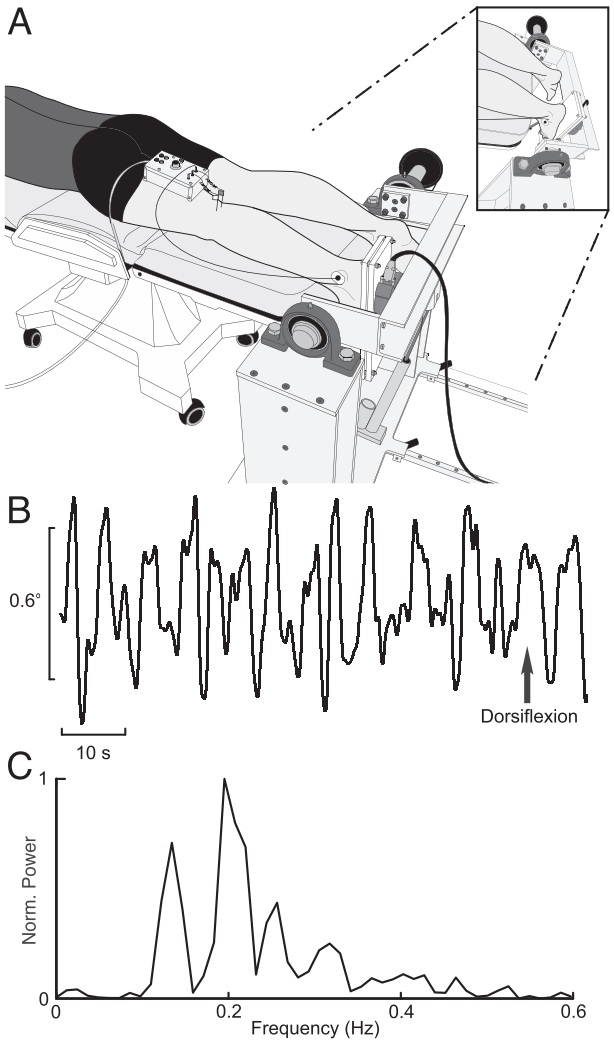

Fig. 1. Apparatus and stimulus profile. (A) The ankle joint was manipulated via a custom-built platform for microneurography. (B) 90-s stochastic ankle angle perturbation delivered on each trial. (C) Power spectra of stochastic ankle angle perturbation along with anteroposterior ankle angle power spectrum during quiet standing (unpublished observations).

often accompanied by further sensations experienced by the participant. To confirm whether the muscle was active or quiescent, we additionally recorded surface electromyography (EMG) over the muscle in which each afferent resided (i.e., "parent muscle"). EMG was amplified × 10,000 by a pre-amplifier (NL824, Digitimer, USA) and amplifier (NL820A, Digitimer, USA), then digitized at 2 kHz by a 16-bit A/D board (Power 1401; Cambridge Electronic Design, United Kingdom) and monitored online using Spike2 v.6 software (Cambridge Electronic Design, United Kingdom). In 15/28 of the recordings, participants remained entirely passive (confirmed by the high gain EMG), and in 13/28 of the recordings, participants were instructed to hold a low-level plantar flexion contraction. Based on a previous report (Hoffman et al., 2009), the plantar flexion torque range (1.9–8.8 Nm) equated to ~2–7% of maximal voluntary contraction during the active task.

Signal analysis and processing

Tibial nerve recordings were amplified × 10,000 and band-pass filtered between 0.3 and 10 kHz (custom-built Yale microneurography amplifier, New Haven, USA). The neural data were digitized by an A/D board at a sample rate of 20 kHz (Spike2 and Power 1401 interface). An audio monitor was used for audio presentation of the neural signal. The majority of action potentials encountered when using microneurography to record somatosensory afferent activity have an initial, positive double-peaked morphology (Inglis et al., 1996). Action potential sorting and morphological analysis was performed off-line using the Spike2 template matching software (see insets showing 100 overlaid spikes in Fig. 2). This software allowed us to retrieve individual spikes under full visual control using waveform template matching. Afferent spike trains, as well as the stimulus waveform were exported to MATLAB (The MathWorks Inc., Natick, MA, USA) for spectral analysis using the hybrid data routine packaged with the NeuroSpec 2.0 (FFT segment length: 6.5536 s; frequency resolution: 0.1526 Hz) software suite. This routine was used to extract the phase and coherence spectra (Rosenberg et al., 1989; Halliday et al., 1995; Amjad et al., 1997) between the input (ankle velocity) and output (afferent spikes).

Ankle perturbation stimulus

Once a spindle was identified, we placed the participant's foot into a custom-built ankle platform (avg. loading force = 34.6, ±21.7 N), designed specifically for microneurography experiments on the tibial nerve (see Fig. 1A). To assist with the loading of the foot, the entire apparatus sat on linear slides that locked into position. A rotary carriage, supported by pillow block mounts on either end was coupled to a linear motor (Model: 36/60-B.125-DYN502-8-2NO-ST4/4, Ultra Motion, Cutchogue, NY, USA) that was fixed to the base of the apparatus. When the linear motor extended, the carriage plantar flexed the ankle, and when the motor retracted the carriage dorsiflexed the ankle. A six-axis load cell (Model: JR31000N125, Multi-Axis Load Cell Technologies, Woodland, CA, USA) was fixed on one side to the rotary carriage, and on the other side to a flat acetal plastic footplate that the participant's foot was loaded against during stimulation. The six channels of the load cell (Fx, Fy, Fz, Mx, My, Mz) were digitized at 100 Hz via an A/D board (Spike2 and Power 1401 interface). A rotary incremental encoder (Model: DRS20-1FK08192, SICK STEGMANN Inc., Dayton, OH, USA) coupled to one end of the rotary carriage via a belt drive system provided digital angular feedback signals to the motion control system (quadrature encoder angular resolution: 0.00197°/count). The motion control system was comprised of a Universal Motion Interface (UMI-7774, National Instruments, Austin, TX, USA), which relayed signals to a motion control card (PXI-7350, National Instruments, Austin, TX, USA) linked with real-time controller (PXI-8106, National Instruments, Austin, TX, USA). The ankle actuator platform was

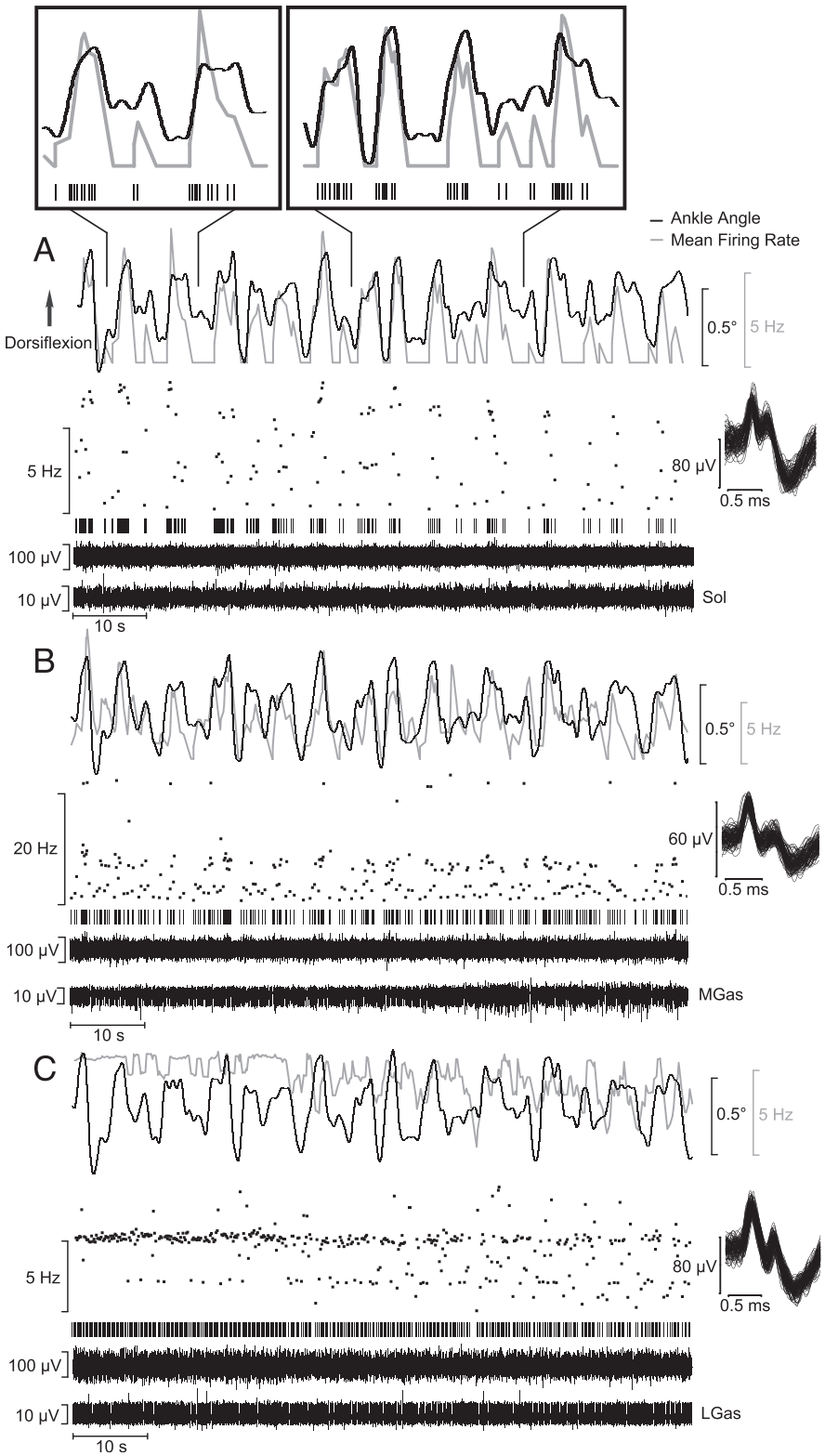

Fig. 2. Spiking activity of single muscle spindles. (A) Soleus, (B) MGas, (C) LGas. Top: Black traces show ankle angle, and grey traces show mean firing rate. Middle: instantaneous firing rate. Bottom: raw neurogram and EMG (inset right: 100 overlaid spikes).

programmatically controlled through a virtual instrument created in-house using the LabVIEW 11 NI Motion Control suite (National Instruments, Austin, TX, USA). The PID control loop duration was 62 μs and the random motion contour was specified at 10 ms intervals (100 Hz); the NI motion controller processed the contouring data by splining between successive points. The platform motion signal was a 90-s, random ankle rotation (peak-to-peak = 0.7°, mean power frequency = 0.28 Hz, band-passed white noise between 0.1 and 0.5 Hz; Fig. 1B, C). This ankle rotation profile was designed to mimic the range of anteroposterior ankle rotation observed during quiet standing in our laboratory. While there is typically still some power below 0.1 Hz, however, we cannot adequately resolve lower frequencies due to FFT windowing at 6.5536 s (frequency resolution of 0.1526 Hz; see below). Ankle angle from the encoder was sent as an analog voltage signal to an A/D board (Spike2 and Power 1401 interface, Cambridge Electronics Design, UK) and digitized at 100 Hz together with the load cell and neural recording channels for analysis; ankle angle was differentiated and up-sampled to 10 kHz offline in MATLAB (The MathWorks Inc., Natick, MA, USA) for further processing.

Statistical analysis

Coherence and phase estimates between afferent spike trains and ankle velocity were derived using MATLAB scripts (NeuroSpec2.0) based on the methods described by Rosenberg and colleagues (1989). Coherence estimates were calculated for each trial using FFT segments of 2^{16} data points (6.5536 s; 13 segments per 90-s trial) with 95% confidence limits. Phases were considered only at frequencies exhibiting significant coherence, since this variable is only meaningful when a relationship exists (i.e., significant coherence is present) between the two signals being compared (Halliday et al., 1995). We tested for an effect of contraction state (active, passive), and muscle (Sol, Gas) on the dependent variable, coherence. Data from individual trials were concatenated across muscles to investigate the effect of contraction level, and across contraction levels to investigate the effect of muscles. Sig-

nificant changes in coherence between contraction levels and muscles were identified using difference of coherence (DoC) tests (Amjad et al., 1997). The DoC test is applied on Fisher transformed coherence values, evaluated over the 0.1526–0.6104 Hz frequency range (corresponding to the bandwidth of the ankle perturbation profile), and compared to a χ^2 distribution with $k-1$ degrees of freedom (k is the number of experimental conditions; Amjad et al., 1997). The significance level was set at $p < 0.05$.

RESULTS

We observed that a population of muscle spindles of the triceps surae are capable of providing precise feedback about ankle angle during small, slow rotations similar to those experienced during quiet standing (Fig. 2). For muscle spindles that accurately coded ankle movements (e.g., see Fig. 2A, B), firing rate modulation between ~5 and 10 Hz was observed throughout the 90-s trials, even during movements much smaller than the peak-to-peak (0.7°) displacements. Taking a linear systems approach, we quantified the coherence and phase spectra between the stimulus (ankle platform velocity) and the evoked afferent spike train (Rosenberg et al., 1989; Halliday et al., 1995; Amjad et al., 1997). Significant coherence was observed for at least one frequency component associated with the applied ankle motion for 4/5 Sol spindles (10 trials), 1/2 MGas spindles (five trials), and 2/5 LGas spindles (two trials) (Fig. 3A). We first compared muscle spindle coding during active and passive trials by concatenated recordings across muscles (Sol vs. Gas). A DoC test revealed that voluntary contraction of the parent muscle significantly reduced coherence at the 0.31 Hz component (Fig. 3B); we note this frequency component (0.31 Hz) is closest to the mean power frequency of the stimulus (0.28 Hz). To compare differences in spindle coding accuracy across muscles, we concatenated across active and passive trials. A pooled DoC test revealed significantly greater coherence at 0.15, 0.31 and 0.46 Hz for Sol compared to Gas (Fig. 3C). When coherence was significant, an average phase lag (re: velocity) of 54.8° (SD = 25.3°) indicated muscle spindle responses were between ankle velocity and position.

We instructed participants to hold a constant low-level contraction, but in all trials, EMG amplitude was modulated (i.e., muscle activation was not strictly static; see Fig. 4A). To determine if muscle activation (root mean square (RMS) of the EMG), was correlated to the ankle stimulus (compare Fig. 4A, 4B), we computed the coherence spectra between ankle velocity and RMS EMG (time window 0.5 s) for every active contraction trial (Fig. 4C). For the majority of the active contraction trials ($n = 8$) the EMG amplitude was not correlated with the ankle stimulus. We found that five out of the 13 active trials exhibited significant coherence between ankle velocity and parent muscle RMS EMG for at least one frequency component. For two of these trials, significant coherence was only seen at a single frequency component, which was the closest to the stimulus mean power frequency. In all cases, the EMG amplitude was modulated (i.e., not strictly static, even when uncorrelated to the stimulus; see Fig. 4A).

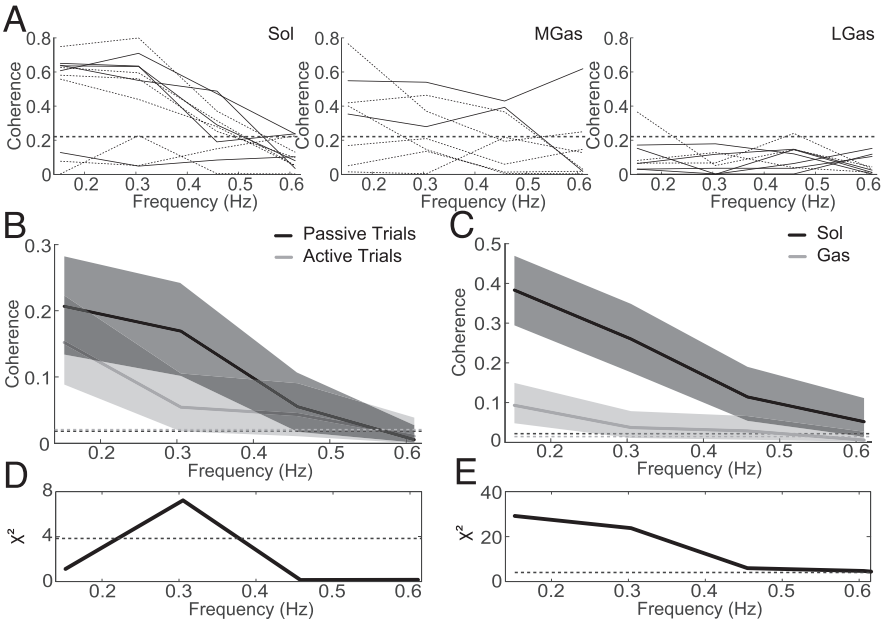

Fig. 3. Population results. (A) Coherence spectra for all 90-s trials. Left: Sol, middle: MGas, right: LGas. Solid lines = active, dotted lines = passive. Horizontal dashed lines denote significance level at $p = 0.05$. The middle row of panels depicts the comparison of coherence spectra between active and passive trials (B), and the different muscles (C). Shaded areas correspond to 95% confidence intervals. The bottom row of panels depicts the difference of coherence χ^2 test results for the comparisons between active and passive trials (D), and the different muscles (E).

DISCUSSION

Summary of findings

We observed that a population of muscle spindles in the human triceps surae are sensitive enough to provide valuable sensory feedback for upright balance control. Afferent responses lagged ~55° behind the stimulus velocity; with a 0° lag representing velocity coding and a 90° lag representing coding in phase with position, a phase lag of ~55° means that responses were delayed with respect to velocity but led position. This phase lag for passive muscle stretching is in agreement with the literature (Roll et al., 2000; Ribot-Ciscar et al., 2002, 2003). When participants held a low-level contraction during the ankle movements, coding of ankle velocity decreased to a significant degree at the frequency component nearest the mean power frequency of the stimulus. Finally, we observed that soleus had the most sensitive spindles, which potentially explains why the anatomical density of spindle afferents is over twice as high in the

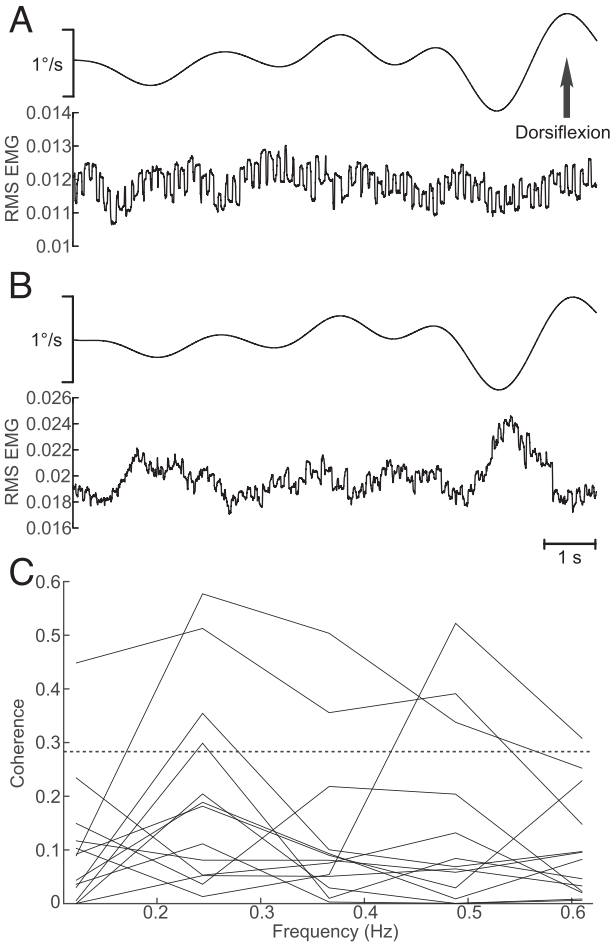

Fig. 4. The relationship between mechanical stimulus and EMG amplitude during active trials. (A) Sample data from an active contraction trial where the stimulus was uncorrelated to the RMS EMG. (B) Sample data from an active contraction trial where the stimulus was correlated to the RMS EMG. (C) Coherence spectra computed between stimulus velocity and RMS EMG for each active contraction trial. Upward deflection of the ankle velocity traces corresponds to dorsiflexion. Horizontal dashed line denotes a significance level of $p = 0.05$.

soleus relative to the gastrocnemius muscles (Voss, 1971; Banks, 2006). Soleus muscle spindles are at an advantage over those in the gastrocnemii because the soleus muscle is monoarticular, and therefore, its passive fascicle length changes depend only on ankle joint angle.

Patterning of muscle spindle sensitivity, innervation density, and muscle activation

As expected, the most sensitive afferents for encoding ankle rotations resided within the soleus. Perhaps non-coincidentally, soleus is tonically active during standing, medial gastrocnemius is both on and off with ballistic, '*catch and throw*' activity, and lateral gastrocnemius is rarely active (Joseph and Nightingale, 1952; Monster et al., 1978; Héroux et al., 2014). Therefore, the pattern of muscle afferent sensitivities we observed for the Sol vs. Gas muscles also aligns with the functional requirements of this muscle group observed during upright standing. The soleus is also a monoarticular muscle, operating only around the ankle joint, while the gastrocnemii are biarticular, operating around both the ankle and knee. Given this anatomy, muscle fascicle length changes in soleus are directly related to ankle angle, however, fascicle length changes in the gastrocnemii can result from movement at either the ankle or the knee, leading to ambiguity in the coding of joint movement (Sturnieks et al., 2007). Unfortunately, ultrasonographic studies of muscle fascicle length changes in passive and active triceps surae are sparse, and also have used much larger rotations of ankle than those in the present study (Maganaris et al., 1998; Herbert et al., 2002). Maganaris et al. (1998) observed a ~30% reduction in muscle fascicle length in the passive soleus and gastrocnemii muscles alike over the range of 15° of dorsiflexion to 30° of plantar flexion. However, whether more subtle differences exist between the muscles for the smaller, slower movements associated with upright standing remains to be investigated.

Reduced spindle coding with parent muscle contraction

When plantar flexor muscles are passively stretched, as we have observed here, and as observed in ankle dorsiflexor muscles for larger, faster movements (Roll et al., 2000; Ribot-Ciscar et al., 2002, 2003), muscle spindles can provide a reliable representation of ankle movement that lags velocity and leads position. However, during actual standing, changes in the mechanical state of the parent muscle and tendon, as well as the introduction of α- (and likely γ-) motoneuron drive during isotonic, eccentric, and concentric active muscle contractions complicates matters considerably (Dimitriou and Edin, 2008a, 2008b; Dimitriou and Edin, 2010). While our task likely did not mimic γ-motoneuron activation associated with standing balance, we did observe that voluntary, (nearly) constant α-motoneuron drive during the ankle oscillations acted to reduce muscle spindle coding accuracy, as indexed by the level of coherence between the spike train and stimulus waveform. In the present study, any potential gamma coactivation should be thought of as dynamic, rather than strictly static (see Goodwin et al., 1975). Goodwin and colleagues (1975) observed that introducing static and dynamic low-level stimulation of the fusimotor system resulted in a decrement in primary ending coding of vibration below 30 Hz; above this frequency, the response gain was enhanced, suggesting that fusimotor drive shifts the sensitivity of muscle spindles to higher frequencies (or potentially, from coding position/velocity, to coding for acceleration – see below). We have two non-mutually exclusive hypotheses for why this might be the case. First, α-motoneuron drive will cause increased muscle stiffness, making the already small amount of muscle tissue deformation from our stimulus even smaller, thereby reducing the signal that muscle spindles are attempting to transduce. This is supported by the observation that the percentage change in triceps surae muscle lengths for the same range of ankle rotation is smaller during maximal contraction (Maganaris et al., 1998). However, the same result would be predicted under the hypothesis that muscle shortening from voluntary

α-motoneuron drive caused unloading of the intrafusal muscle fibres that went uncompensated for by γ-motoneuron activation or that γ-motoneuron co-activation is not sufficient to keep the spindles sensitive during passive stretch. An alternate viewpoint is that reduced coding accuracy would be predicted because fusimotor drive to the muscle spindles would provide, in addition to the ankle movement induced muscle stretching, a second input to the muscle receptors. Consequently, the firing rate of the recorded muscle spindles would be driven by (and correlated with) both the fusimotor drive and the stretching of the muscle receptors, leading to a decreased correlation between the ankle movement and muscle spindle firing rate. Beyond this speculation, the current data do not allow us to distinguish between these hypotheses.

Limitations and conclusion

Human lower-limb muscle spindle activity has only been investigated using much larger movements of the ankle dorsiflexors, which are supplied by the common fibular nerve (Roll et al., 2000; Ribot-Ciscar et al., 2000, 2002, 2003; Hospod et al., 2007; Day et al., in press). Only two prior reports provide minimal data on muscle afferents located in the triceps surae, but no controlled mechanical stimulation was ever applied (Hagbarth and Vallbo, 1969; Aniss et al., 1988). Despite rotating the ankle joint with a random oscillation characteristic of upright standing, and with the parent muscle in both passive and active states, we acknowledge that this is different from having participants actively engaged in balance control, as our participants were lying prone. Only dorsiflexor muscle spindle afferents have been recorded from during actual standing previously (Burke and Eklund, 1977; Aniss et al., 1990). In addition, we must note that our sample size for this experiment is low, further reflecting the technical difficulty of these experiments. To gain further insight into the role that α- and γ-motoneuron drive plays in shaping lower-limb muscle spindle activity, a critical next step is to compare afferent activation patterns from the present study against those obtained during an active balancing task, if not during actual standing. For example, when humans are engaged in an actively controlled upper-limb tasks (e.g., grasping a object, pressing buttons), recent research has implicated that the fusimotor system causes a phase advance in the response, leading to spindles coding for parent muscle velocity ~160 ms in the future (i.e., they begin coding for muscle acceleration and velocity). Due to this, it has been suggested that muscle spindles serve as embedded forward models during the control of movement, predicting future states of their parent muscles (Taylor et al., 2006; Dimitriou and Edin, 2010; Prochazka and Ellaway, 2012; Prochazka, 2015). Whether muscle fascicle acceleration coding occurs in triceps surae muscle spindles if participants are actively engage in a balancing task remains to be determined. However, our observations of plantar flexor muscle spindles, and previous observations on Tibialis Anterior muscle spindles (Roll et al., 2000; Ribot-Ciscar et al., 2000, 2002, 2003; Hospod et al., 2007; Day et al., in press), support the notion that in a passive state, lower limb muscle spindles supply useful feedback regarding ankle position and velocity. Finally, counter to previous reports based on ultrasonography during upright balance (Loram et al., 2004, 2008), we suggest triceps surae muscle spindles may comprise an important component of the human standing balance control loop.

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