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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