Motor unit recruitment and firing rate in medial gastrocnemius muscles during external perturbations in standing in humans

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Pollock CL, Ivanova TD, Hunt MA, Garland SJ. Motor unit recruitment and firing rate in medial gastrocnemius muscles during external perturbations in standing in humans. J Neurophysiol 112: 1678–1684, 2014. First published July 2, 2014; doi:10.1152/jn.00063.2014.—There is limited investigation of the interaction between motor unit recruitment and rate coding for modulating force during standing or responding to external perturbations. Fifty-seven motor units were recorded from the medial gastrocnemius muscle with intramuscular electrodes in response to external perturbations in standing. Anteriorly directed perturbations were generated by applying loads in 0.45-kg increments at the pelvis every 25–40 s until 2.25 kg was maintained. Motor unit firing rate was calculated for the initial recruitment load and all subsequent loads during two epochs: 1) dynamic response to perturbation directly following each load drop and 2) maintenance of steady state between perturbations. Joint kinematics and surface electromyography (EMG) from lower extremities and force platform measurements were assessed. Application of the external loads resulted in a significant forward progression of the anterior-posterior center of pressure (AP COP) that was accompanied by modest changes in joint angles (<3°). Surface EMG increased more in medial gastrocnemius than in the other recorded muscles. At initial recruitment, motor unit firing rate immediately after the load drop was significantly lower than during subsequent load drops or during the steady state at the same load. There was a modest increase in motor unit firing rate immediately after the load drop on subsequent load drops associated with regaining balance. There was no effect of maintaining balance with increased load and forward progression of the AP COP on steady-state motor unit firing rate. The medial gastrocnemius utilized primarily motor unit recruitment to achieve the increased levels of activation necessary to maintain standing in the presence of external loads.

Motor unit; muscle activity; postural control in standing; perturbation

Gradation of muscle force is controlled by a combination of motor unit recruitment and rate coding (Heckman and Enoka 2012). Muscles differ in their use of motor unit recruitment versus rate coding to modulate force, possibly related to the muscle fiber composition and characteristics of muscle contraction (De Luca et al. 1982; Kukulka and Clamann 1981). For instance, during ramp isometric contractions, muscles composed of a mix of fiber types have been shown to utilize motor unit recruitment throughout a wider range of available force than muscles consisting primarily of slow-twitch fibers (Kukulka and Clamann 1981). The characteristics of the muscle contraction that can influence the interaction of motor unit recruitment and rate coding include joint angle and muscle length (Ballantyne et al. 1993; Kennedy and Cresswell 2001), speed of muscle contraction (Desmedt and Godaux 1977), the nature of the external load (Pascoe et al. 2013), and the type of contraction used (concentric, eccentric, or isometric; Duchateau and Baudry 2014). All of the aforementioned studies were performed in sitting, and the interaction between motor unit recruitment and rate coding for modulating force during standing or in response to standing external perturbations has not been explored. Standing balance integrates multiple sensory inputs, and the synaptic inputs on the motoneurons of postural muscles in standing differ from those of isometric ramp contractions (Jacobs and Horak 2007). Therefore, motor unit behavior in a functional task of standing and withstanding external perturbations must be examined in a task-specific paradigm.

Maintaining standing balance requires control of postural muscles; specifically, the ankle plantarflexors play a critical role in controlling anterior-posterior movements of the center of mass (COM) within the base of support. It has been suggested that the soleus muscle is the main muscle controlling balance during quiet standing, while the gastrocnemius muscle plays an increasingly active role when the COM travels more anterior to the ankle joint (Di Giulio et al. 2009). Motor unit firing rate of the soleus muscle has been shown to demonstrate rather modest modulation during quiet stance with eyes open or closed (Mochizuki et al. 2007). Conversely, motor unit activity of the medial gastrocnemius muscle has been shown to be intermittent, with recruitment of motor units primarily during forward sway of the center of pressure (COP) in quiet standing (Vieira et al. 2012).

Forward sway and the associated length changes of the muscles about the ankle (both plantarflexors and dorsiflexors) have been suggested to provide the sensory information that drives modulation of the gastrocnemius muscles during quiet standing (Di Giulio et al. 2009; Tokuno et al. 2008; Vieira et al. 2012). Plantarflexor activity in standing has been shown to precede anterior displacement of the COP (Masani et al. 2003). However, it has been shown that compared with the COM displacement the velocity of COM during quiet standing is more associated with activation of the ankle plantarflexors in anticipation of a forward sway (Masani et al. 2003). Responding to perturbations in standing has been shown to integrate both short-loop reflexive behavior and long-loop reflexive behavior that incorporates supraspinal centers (Jacobs and Horak 2007). The relative weighting of these inputs has been suggested to change with increased challenge to standing balance (Gibbs et al. 1995; Horak 2006). However, it remains unclear as to how the medial gastrocnemius muscle modulates force in response to standing perturbations. The purpose of this
study was to determine 1) whether increased firing rate and recruitment of motor units in medial gastrocnemius muscle occur during the maintenance of standing balance with increasing levels of anteriorly directed loads and 2) whether the medial gastrocnemius muscle utilizes motor unit recruitment and rate coding in response to abrupt external perturbations of equal magnitude superimposed on the anteriorly directed loads. Specifically, we hypothesized that the increased force required from the medial gastrocnemius to resist the external loads would increase both motor unit recruitment and firing rate. During the dynamic response to perturbation, we hypothesized that motor unit recruitment would occur with each perturbation and motor unit firing rate would increase with subsequent perturbations experienced with increasing levels of anterior progression of the COP.

METHODS

Six healthy adults (3 women, 3 men; 42 ± 8.8 yr of age, 60.8 ± 9.0 kg, 166.5 ± 10.5 cm) participated on three separate occasions. Individuals were excluded if they had any health conditions that negatively impacted mobility (e.g., severe osteoarthritis, neurological conditions). The study conformed to the standards set by the latest revision of the Declaration of Helsinki and was approved by the University of British Columbia Clinical Research Ethics Board.

Experimental protocol. Participants stood with their feet shoulder width apart, with each foot on a separate force platform (AMTI OR6-6, Advanced Mechanical Technology, Watertown, MA). Baseline quiet standing data were collected for 30 s; then participants were instructed to lean as far forward as possible without needing to take a step to regain their balance. This point represented the perceived anterior limit of stability (LOS). LOS trials were performed twice, and the maximum anterior excursion was used as the perceived anterior LOS.

A belt was secured around the pelvis of each participant and was attached to a horizontal cable in front of the participant. External loads were applied via a cable-pulley system (1.6-mm 7 × 7 galvanized aircraft cable, graded for up to 41 kg with a steel pulley mounted on a tripod) attached to the front of the belt (Fig. 1). Participants remained standing in comfortable stance with each foot on a separate force platform as external loads of 0.45 kg were applied five times through the belt by being dropped into an attached basket from ~40 cm every 25–40 s (random timing); the weights were not removed from the basket, so the maintained load increased incrementally until 2.25 kg was reached. The calibrated weights were made from concrete gravel pellets housed in a soft cover bag. A screen in front of the participants prevented them from seeing when the loads were dropped. Application of the load was detected by a force transducer in line with the cable (Fig. 1). Subjects were instructed to maintain their standing balance without taking a step in response to each perturbation. All participants experienced a perturbation in a practice trial prior to the data collection.

Motor unit recordings. Motor unit potentials were recorded intramuscularly with fine-wire bipolar electrodes. Bipolar electrodes were custom made with three 50-μm stainless steel fine wires (California Fine Wire, Grover Beach, CA) fastened together with cyanoacrylate adhesive and inserted into a disposable 2-cm, 25-gauge hypodermic needle (Becton Dickinson, Franklin Lakes, NJ). A hook, ~2 mm in length, was formed at the recording end of the electrode. The three-wire electrode allowed selection of a recording from three possible bipolar configurations and choice of the optimal configuration based on signal-to-noise ratio. The electrodes were autoclaved prior to use for 25 min at 120°C. The needle was used to insert the electrode into the medial aspect of the medial gastrocnemius to a depth of ~2 cm and was extracted, leaving the fine-wire electrode in the muscle. Two electrodes were inserted into the medial gastrocnemius muscle of each leg (4 electrodes in total), with ~5–7 cm separating the electrodes.

The electrode position was adjusted to ensure that at least one motor unit potential was identifiable from each medial gastrocnemius muscle (in some trials >1 motor unit was identifiable per electrode). Once this was achieved, the electrodes were not moved again. Motor unit recordings were sampled at 20 kHz.

Surface EMG recordings. Bipolar electrodes (1-cm interelectrode distance) were used to record surface EMG bilaterally from the medial gastrocnemius, soleus, rectus femoris, biceps femoris, and lumbar erector spinae bilaterally. Surface EMG (Delsys, Natick, MA) was sampled at 2,000 Hz and saved for off-line analysis.

Kinetic and kinematic data. Kinetic data were collected with two floor-mounted force platforms (detailed above), sampled at 2,000 Hz. Anterior-posterior (AP) COP displacements and velocity (the derivative of AP COP displacement) with each perturbation were calculated from raw force platform data. Twenty-two passive reflective markers were affixed to the participants according to a modified Helen Hayes marker set (Kadaba et al. 1989) to allow for motion capture of the arms, trunk, and legs bilaterally. Eight high-speed digital cameras (Raptor-E, Motion Analysis, Santa Rosa, CA) sampled the movement of the reflective markers at 100 Hz. Kinematic data were analyzed with a custom-written program (MathWorks, Natick, MA) developed in a previous study to quantify lower extremity kinematics during movement (Pollock et al. 2012). Body segment angles were calculated only in the sagittal plane for the ankle, knee, and hip (Fig. 1). External torque applied about the ankles was calculated as the product of the perpendicular distance of the AP COP from the ankle joint center and the vertical component of the ground reaction force.

Data analysis. Motor unit identification was performed in Spike2 (Cambridge Electronic Design, Cambridge, UK) with a template-matching algorithm that classifies motor unit potentials according to the shape and amplitude of the motor unit potentials. Visual inspection of the data allowed the identification of instances of misclassification; sections of data that contained misclassifications were eliminated from the analysis.

Motor unit firing rate was calculated during two epochs: 1) the dynamic response to the perturbation—mean of the first three inter-spike intervals (ISIs) directly following each load drop and fastest ISI of the first three ISIs—and 2) maintenance of steady state between perturbations—mean ISI over a 5-s epoch taken between 5 s after the load drop and 1 s prior to the next load drop. The mean, standard deviation, and coefficient of variation (CV) of the ISIs during this 5-s
was compared to steady state with paired $t$-tests. The RMS amplitudes of surface EMG data were calculated with respect to quiet standing. Root mean square (RMS) of the surface EMG for each muscle was calculated during the aforementioned time periods of interest, for 500 ms during the dynamic response following load drop and for the same 5-s epoch used to measure motor unit ISI during the maintenance of steady state between perturbations. RMS was normalized to quiet standing prior to the application of the first load. The excursion of the AP COP was calculated and converted to a percentage of the LOS. The velocity of the AP COP excursion during the dynamic response to load drop was calculated as the derivative of the AP COP signal. The peak external torque at the ankle during the dynamic response to load drop and mean external torque at the ankle during steady state were calculated and normalized to the external torque calculated during quiet stance. The changes in ankle, knee, and hip angle in the sagittal plane in response to the external loads were calculated with respect to quiet standing.

Statistical analysis. Statistical analysis was performed with SPSS v.20.0 (SPSS, Chicago, IL). ISI data were not normally distributed; therefore, Kruskal-Wallis analysis of variance (ANOVA) tests were performed on the median motor unit ISI duration to test for the effect of load level (1–5) on motor unit firing rate during the dynamic response to load drop, the median motor unit firing rate was significantly slower at the initial recruitment load (150 ms, IQR 123–170 ms) than during the dynamic response to subsequent load drops (110 ms, IQR 90–125 ms, $P < 0.001$) or during the steady-state discharge at the same load (125 ms, IQR 120–143 ms, $P = 0.001$). The fastest ISI (84 ms, IQR 70–103 ms) was significantly shorter than the average of the first three ISI at each load (Fig. 4, $P < 0.01$). There was also a significant effect of load on the fastest ISI, with the fastest ISI of load 4 being significantly longer than all other load levels (Fig. 4).

Maintenance of steady state between perturbations. As with the dynamic response to the load drop, there was no significant modulation of the motor unit firing rate in response to the load drop. Some motor units were derecruited in the steady-state period after the dynamic response to load drop on the recruitment load (total $n = 10$) yet discharged more steadily after the next load drop and for all subsequent loads (Table 1).

### Table 1. Motor unit recruitment by load level

<table>
<thead>
<tr>
<th>Load</th>
<th>Dynamic response</th>
<th>Steady state</th>
<th>Dynamic response (derecruited in steady state)</th>
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<td>18</td>
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<tr>
<td>Total</td>
<td>40</td>
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epoch were calculated. Since it has been shown that motor unit behavior can differ between that observed at initial recruitment and that when a motor unit is already firing (Van Cutsem and Duchateau 2005), motor units were analyzed at the recruitment load separately from the subsequent loads. Motor units that were active in the dynamic response to load drop and during maintenance of steady state at the same load level were analyzed to determine the extent of modulation of the motor unit firing rate in response to the load perturbation. In total, 57 motor units were identified (yield of 1–4 motor units from each leg) and were compared for the effect of load level (1–5) and side (right, left) with the fastest ISI, with the fastest ISI of load 4 being significantly longer than all other load levels (Fig. 4).

**Results**

Overview of motor unit recruitment. In total, 57 motor units were identified (yield of 1–4 motor units from each leg) and followed over successive loads once recruited. Motor units were collected successfully from 12 of the 18 experiments performed. Motor units were recruited either during the dynamic response to load drop (total $n = 40$) or during the steady-state periods (total $n = 17$). Only two of the recorded motor units were active in quiet stance prior to the first load drop. Some motor units were derecruited in the steady-state period after the dynamic response to load drop on the recruitment load (total $n = 10$) yet discharged more steadily after the next load drop and for all subsequent loads (Table 1).

Dynamic response to the perturbation. Figure 2 shows two representative examples of the dynamic response to load drop. The mean of the first three ISIs immediately after load drop was similar irrespective of the load at which the motor unit was recruited (Fig. 3A, $P = 0.76$). During subsequent load drops, there was also no significant difference in the motor unit firing rate across load levels (Fig. 3B, $P = 0.97$). However, for the 40 motor units recruited during the dynamic response to load drop, the median motor unit firing rate was significantly slower at the initial recruitment load (150 ms, IQR 123–170 ms) than during the dynamic response to subsequent load drops (110 ms, IQR 90–125 ms, $P < 0.001$) or during the steady-state discharge at the same load (125 ms, IQR 120–143 ms, $P = 0.001$). The fastest ISI (84 ms, IQR 70–103 ms) was significantly shorter than the average of the first three ISI at each load (Fig. 4, $P < 0.01$). There was also a significant effect of load on the fastest ISI, with the fastest ISI of load 4 being significantly longer than all other load levels (Fig. 4).

Maintenance of steady state between perturbations. As with the dynamic response to the load drop, there was no significant modulation of the motor unit firing rate in response to the load drop. Some motor units were derecruited in the steady-state period after the dynamic response to load drop on the recruitment load (total $n = 10$) yet discharged more steadily after the next load drop and for all subsequent loads (Table 1).
effect of increasing load on the motor unit firing rate (Fig. 4, \( P = 0.80 \)). The consistency in motor unit firing rate in the steady-state phase between perturbations is demonstrated in Fig. 5 in a representative subject. The CV of motor unit firing rate was significantly faster during the dynamic response compared with motor unit duration of the first 3 ISIs in response to subsequent load drops (\(^* P < 0.05 \)).

Modulation between dynamic response to perturbation and maintenance of steady state. Although there was no effect of load on motor unit firing rate, there was significant modulation of the motor unit firing rate in the dynamic response to the load drop when the motor units were already active prior to perturbation (Fig. 2). The motor unit firing rate was significantly faster (110 ms, IQR 90–125 ms) during the dynamic response than during steady state after subsequent load drops (15.85%, IQR 11.97–19.30%, \( P < 0.01 \)).

Kinetic, kinematic, and surface EMG response to perturbations. None of the kinetic, kinematic, or surface EMG data were different between the left and right legs of participants (\( P > 0.1 \)), reflecting symmetrical responses to the external loads. Therefore, data from both legs were averaged (Fig. 6). The application of the external loads resulted in a significant increase in external torque applied to the ankle both during the dynamic response to load drop (peak torque, \( P < 0.001 \)) and during steady state (mean torque, \( P < 0.01 \)) (Fig. 6A). This was associated with a significant forward progression of the AP COP with increasing load, which culminated in an anterior excursion of COP of 46.3 ± 22.8 mm by the fifth load level, an excursion representing 41.7 ± 21.6% of the LOS (Fig. 6A). In contrast to AP COP positions, there was no significant effect of load level on AP COP velocity during the dynamic response to load drop (\( P = 0.21 \)).

The RMS amplitude of each muscle during steady state, normalized to quiet stance, is presented in Fig. 6B. There was a significant effect of increasing load on RMS amplitude in medial gastrocnemius (\( P = 0.02 \)), soleus (\( P < 0.01 \), and tibialis anterior (\( P < 0.01 \)) but not in rectus femoris (\( P = 0.19 \)), biceps femoris (\( P = 0.21 \)), or lumbar erector spinae (\( P = 0.15 \)). Compared among muscles at each load, the RMS amplitude of the medial gastrocnemius muscle increased significantly more than soleus, tibialis anterior, biceps femoris, rectus femoris, and lumbar erector spinae at each load (Fig. 6B, \( P \leq 0.05 \)). The RMS amplitude of the medial gastrocnemius muscle during the dynamic response to perturbation was significantly larger than during steady state (\( P < 0.01 \)).

Within each joint, there was a significant effect of increasing load on hip extension (\( P = 0.01 \)) and knee flexion (\( P = 0.02 \)) but only a trend for ankle dorsiflexion (\( P = 0.07 \)). However, the changes in ankle, knee, and hip position in response to the external load from quiet stance were small (<3°; Fig. 6C). The standard error of joint excursions at each load level was <1°.

DISCUSSION

The aim of this study was to examine motor unit recruitment and rate coding in the medial gastrocnemius muscle in response to external perturbations experienced under increased levels of challenge to standing balance. Multiple kinetic and kinetic measures supported the potency of the postural manipulations. The loads resulted in a symmetrical response in the two legs including a gradual increase in external ankle torque, forward progression of the COP, and small but significant increases in hip extension and knee flexion. There was preferential activation of the medial gastrocnemius muscle, which was significantly higher than all other muscles recorded. Motor units were recruited both in the dynamic response to load drop and during the steady-state periods between external loads. Upon initial recruitment, motor units demonstrated a lower firing rate than at subsequent loads. Thereafter, rate coding was only observed as a transient increase in firing rate in response to each perturbation, followed by a return to a lower firing rate that did not change with increases in static anterior loads maintained at the pelvis. Considering the significant increase in the amplitude of medial gastrocnemius muscle EMG with increased static loading, this suggests that motor unit recruitment may have been the prevailing means of force gradation within this postural task.

Fig. 3. Duration of the motor unit first 3 ISIs during dynamic response. Box plot (median) of motor unit ISIs during dynamic response grouped by recruitment vs. subsequent loads. A: motor unit behavior at initial recruitment based on whether recruited at load 1, 2, or 3–5; B: motor unit behavior with subsequent loads where motor units were active prior to perturbation. Increased level of perturbation did not influence firing rate (loads 3–5 combined because of lower number of motor units identified at these perturbation levels). At recruitment motor units demonstrated increased duration of the first 3 ISIs during dynamic response compared with motor unit duration of the first 3 ISIs in response to subsequent load drops (\(^* P < 0.05 \)).

Fig. 4. Motor unit firing behavior after initial recruitment, with subsequent perturbations. Median and interquartile range for motor unit ISI evoked by the perturbation: fastest of first 3 ISIs (gray circles), mean of first 3 ISIs (black circles), followed by ISI during steady state at the next load increment (open circles). Motor units modulated their firing behavior by significantly decreasing the duration of ISI during the dynamic response to load drop compared with ISI during steady state. The duration of the ISI was significantly longer between steady state and the dynamic response to perturbation and between the mean of the first 3 ISIs and the fastest ISI (\(^* P < 0.05 \)). The duration of the fastest ISI during the dynamic response at load 4 was significantly longer than with other perturbations († \( P < 0.05 \)).
The range for motor unit recruitment force during ramp isometric contractions has been shown to differ in muscles with different fiber type compositions and functions (De Luca et al. 1982; Kukulka and Clamann 1981). In the upper extremity, motor unit recruitment occurred up to 80% maximal voluntary contraction (MVC) in the biceps brachii (comprised of 34–61% type I muscle fibers), whereas adductor pollicis (72–91% type I muscle fibers) showed no further recruitment beyond 30–40% MVC (Kukulka and Clamann 1981). However, the soleus muscle, also composed of a large percentage of type I muscle fibers, has shown motor unit recruitment during ramp contractions at forces > 89% MVC (Oya et al. 2009). Similar to biceps brachii, medial gastrocnemius muscle is composed of 47–57% type I fibers (Johnson et al. 1973), and in the present study the medial gastrocnemius muscle showed no significant difference in firing rate in standing during maintenance of steady state across all loads. This suggests a larger role for motor unit recruitment to maintain standing in the presence of a progressive forward movement of the COP and the associated increase in external torque applied about the ankle.

Immediately after each load drop, the behavior of the motor unit showed a transient increase in firing rate compared with steady state after the initial recruitment load. This behavior mirrored the external peak torque at the ankle that was greater than the mean torque when the same load was maintained during standing. There are a number of factors that may influence the modulation of firing rate that occurred only in response to the dynamic perturbation. It is interesting to consider our motor unit findings in the context of Masani et al. (2003), who noted the importance of the AP COM velocity in modulating gastrocnemius activation. As there is no sensory system that directly measures the velocity of the COM, Masani et al. (2003) suggest that an integration of multisensory information at the CNS contributes to the velocity feedback system. In the present study, there was no significant increase in the AP COP velocity or motor unit firing rate during the dynamic response across loads. It is possible that the motor unit firing rate in the medial gastrocnemius muscle following perturbation is related to controlling the COM velocity, which is reflected in the COP velocity during the dynamic response. It is also possible that the consistency of the motor unit discharge across loads may reflect the fact that the perturbations were imposed by a load of equal magnitude (0.45 kg), resulting in a similar magnitude of destabilizing effect (relative to the preceding maintained load).

It has been demonstrated that the reflex excitability of the motoneuron pool is altered by the relative direction of the COP sway in quiet standing, with the H-reflex response being heightened during forward sway (Tokuno et al. 2008). Motor unit activity of the medial gastrocnemius muscle in quiet standing has been shown to be intermittent and phase locked with anterior shifts of the COP (Di Giulio et al. 2009; Vieira et al. 2012). In the standing position, with the COP advanced anteriorly within the base of support, modulation of the preactivated medial gastrocnemius motor unit firing rate immediately after load drop may be related to heightened sensitivity of the Ia afferent input in this forward position (Di Giulio et al. 2009). This is supported by the finding that medial gastrocnemius fascicle lengths were responsive to length changes associated with dorsiflexion when the knee was held at 0° but not when the knee was bent (Wakahara et al. 2009), suggesting an increased responsiveness of the gastrocnemius to length changes when the muscle is at a lengthened position in standing.

Sensory input from stretch of the hip flexors, which would occur as a result of the anterior pull at the pelvis in this paradigm, may have influenced the motor unit firing rate modulation and recruitment of the medial gastrocnemius. The postural reactions of muscles about the ankle and knee in response to perturbations have been shown to be primarily triggered by proprioceptive input from the hip and trunk movement (Bloem et al. 2002). It is interesting to note that on the fourth load (see Fig. 6C) the slight movement toward hip and knee flexion was accompanied by the fastest ISI being significantly longer than with each of the other loads. The interaction between changes in joint position for the proximal joints and medial gastrocnemius motor unit firing rate modulation and recruitment warrants further investigation.

The modest increase in firing rate immediately after load drop in motor units active prior to perturbation may be reflective of the properties of the Achilles tendon. During standing balance the contractile tissue has been shown to be stiffer than the series elastic component, particularly in the Achilles tendon (Loram et al. 2007). This stiffness may have contributed to the limited dorsiflexion at the ankle (<1.5° change; Fig. 6C) and be playing a buffering role for the plantarflexor force in the
dynamic response to perturbation, lessening the need for firing rate modulation.

The muscle activity associated with postural control is modulated by the brain stem with input from Ia afferents and the vestibular system contributing significantly to modulation of this activity level (Creath et al. 2008). Neuromodulation of motoneurons from brain stem inputs has been shown to provide persistent inward currents (PICs) that are known to lower the recruitment threshold of motoneurons, thereby resulting in amplification of the excitatory input and self-sustained firing (Hultborn et al. 2003; Hyngstrom et al. 2007). While speculative, the motor units in the present study fired more consistently once recruited (lower CV of ISI), behavior that is consistent with the influence of PICs on the medial gastrocnemius motor units.

Finally, the activation of motor units was in response to perturbations, and participants were asked to maintain their standing balance while experiencing these perturbations. For this reason the response to the perturbation would be somewhat controlled. Recruitment of new motor units at a slower firing rate may reflect a strategy to meet the demands of the increased perturbation without further destabilizing standing balance as may occur with a faster firing rate. This suggestion is consistent with Desmedt and Godaux (1977), who observed that the fast initial ISI (<17 ms) at recruitment was only present during trials that did not attempt to control the force pattern and subjects simply contracted as fast as possible.

Overall, these results support the possibility of task dependence on the interaction of rate coding and recruitment. Within the present standing perturbation paradigm, rate coding and recruitment were used differently for static maintenance of load than when abrupt dynamic perturbations were experienced. It may be the case that increases in the magnitude of perturbation loads or the nature of the response (e.g., able to take a step in response) could affect the initial firing rate response of newly recruited motor units.

Conclusions. The medial gastrocnemius muscle utilized motor unit recruitment to achieve the increased levels of ankle torque necessary to maintain standing in the presence of external loads. However, there was evidence of modest rate coding during the dynamic response to perturbations that may be attempting to control the velocity of the forward movement associated with perturbations. Multiple sensory inputs are likely integrated to control medial gastrocnemius activation during steady-state maintenance of standing against a load and during abrupt perturbations. Accordingly, these data support the task-dependent nature of motor unit recruitment and rate coding and extend these findings to maintaining standing balance.

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*Fig. 6. Kinetic, surface EMG, and kinematic response to increasing levels of perturbation. Mean and SE are presented for all parameters. A: there was a significant increase in peak torque at the ankle during the dynamic response to the perturbation (black squares), mean torque during the maintenance of steady state (open circles), and forward progression of AP COP expressed as %LOS of the anterior progression of the COP (black asterisks) (†P < 0.05). B: root mean square (RMS) amplitude of surface EMG normalized to preload drop standing for muscles of the lower extremity and low back in response to an anterior pull on the pelvis. There was a significant increase in the RMS amplitude of medial gastrocnemius (GM) and soleus (SOL) and a significant decrease in Tibialis anterior (TA) (†P < 0.05). The gradual increase of biceps femoral (BF) and lumbar erector spine (LES) muscles and the slight decrease in RMS amplitude of the rectus femoris (RF) muscles did not reach significance with increased load levels. The increase in RMS amplitude of medial gastrocnemius was significantly greater than all other muscles at each load level (†P < 0.05). C: joint angle position changes from quiet standing. Ankle dorsiflexion, knee flexion, and hip extension increased with increasing levels of load (†P < 0.05; trend, ‡P = 0.07).
GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


REFERENCES


