**Directionality of force requirements in standing and motor unit recruitment in the ankle plantarflexors**

**Abstract**

**Purpose**: The purpose of this study was to investigate whether regional modulation of the ankle plantarflexors during standing was related to the recruitment of specific motor units associated with force-direction.

**Methods**: Fourteen participants performed a multi-directional leaning task in standing. Participants stood on a force platform and maintained their posture while projecting their center of pressure into five target directions. Motor unit firings were extracted by decomposing high-density surface electromyograms detected from the ankle plantarflexor muscles. The barycentre, defined as the weighted mean of the average rectified values across columns and rows, was used to evaluate the medio-lateral and proximo-distal changes in the surface representation of single motor units between different leaning target directions. A motor unit tracking analysis was conducted to compare groups of motor units that were common and independent (unique) across the target directions.

**Results**: The leaning directions had an effect on the spatial representations of motor units in the medial gastrocnemius and soleus (*p* > 0.05), but not the lateral gastrocnemius (*p* < 0.05). Motor units action potentials were represented in the medial and proximal aspects of the muscles. Further analysis determined that the common motor units across the target directions were recruited in the same spatial locations (*p* > 0.05), whereas newly recruited unique motor units were recruited in different spatial locations (*p* < 0.05).

**Conclusions**: The central nervous system may possess the ability to activate different groups of motor units to meet the force-direction requirements of the leaning task, according to task demands.

**Introduction**

The control of standing posture is a fundamental requirement for many motor tasks. Success in performing many functional daily tasks requires the activation of populations of motor units within various muscles to achieve postural control. For example, forward leaning during standing is achieved by activating motor units within the plantarflexors, comprised of the medial and lateral gastrocnemius (MG and LG) and the soleus (SOL), to prevent forward toppling (Di Giulio et al., 2009). The central nervous system (CNS) relies on two independent mechanisms for the gradation of force; recruitment and rate coding of motor units. While distinct, these two mechanisms are controlled by the same physiological signal (Binder et al., 1996). However, within a motoneuron pool, individual motor units may be recruited independently (Kernell 2003). The likelihood of a motor unit being recruited depends on the relative distribution of synaptic inputs across motoneurons. During uniform synaptic distribution of the muscle, low threshold motor units are found to discharge first with larger threshold units contributing with larger inputs (Henneman et al. 1965; Milner-Brown et al., 1973). However, recent studies have begun to illustrate regionally-specific distribution of muscle activity across the plantarflexor muscles (Kinugasa et al., 2011; Segal & Song 2006; Dos Anjos et al., 2015). This raises the possibility of the CNS utilizing this regionally-specific distribution of synaptic activity across the different motoneuron pools to control recruitment and rate coding of motor units in conjunction with Henneman’s size principle.

Regional modulation of muscle activation appears to be associated with perturbation direction and body positions. During quiet standing, the activation of motor units in the MG appears to be localised in the longitudinal plane (Viera et al., 2011). In addition to localised motor units, the MG motor units are activated intermittently, with recruitment occurring during different body positions (Viera et al., 2012) suggesting that the CNS can preferentially activate the muscles in specific regions to produce the appropriate muscle force during standing. A functional application of this organization has been shown during perturbations in different directions. In previous work, we revealed the ability of the CNS to preferentially activate the different heads of the MG and LG, as well as specific regions within the plantarflexors (Cohen et al. 2020), using averaged rectified values (ARV) on high-density surface electromyography (HDs-EMG).

Josh, I think you could move straight to the last Introduction paragraph from here. The next two paragraphs appear more related to how you have addressed your question rather than to your motivations for addressing it. You could maybe use this text in discussion and/or methods, to indicate readers the approach we used is robust and valid. I am not saying it is not ok but I think it makes Introduction unnecessarily heavier to read.

There appears to be an association between the amplitude distribution in surface EMG and the location of active muscle fibers in pinnate muscles like the ankle plantarflexors. Due to the in-depth oblique architecture of plantarflexors, action potentials travel from the endplates to deep and superficial extremities of the muscle fibers. When detected at skin regions covering the aponeurosis of in-depth pinnate muscles, surface EMGs do not show the propagation of motor unit action potentials (Gallina *et al.*, 2013). However, the amplitude of signals recorded at this skin location appears to be associated with the number of excited fibers beneath the detecting electrodes (Mesinet al., 2011). From HDsEMG it is therefore possible to estimate the location of fibers of fibers of recruited motor unit in both the proximo-distal and medio-lateral directions. The plantarflexor is therefore a very good muscle to assess the association between motor unit recruitment and functional tasks.

Estimating motor units has been traditionally performed using intramuscular electrodes. Although intramuscular electrodes provide authentic characterizations of action potentials of single motor units (Merletti and Farina 2009), their pickup volumes are considerably small (Lower et al., 2006). Even when recording from multiple intramuscular locations, the recording volumes may intersect the boundaries of motor unit territories and is not sufficient to test the hypothesis of regional recruitment of motor units. Therefore, HDs-EMG is a necessary requirement to test our hypothesis of task-related spatialization of motor units. Consequently, we utilized HDs-EMG over the plantarflexor muscles, which has been shown to be remarkably selective (Vieira et al., 2017; 2021).

It would appear that the CNS utilizes the directionally-specific force information of a postural task to modulate force requirements. Uneven distribution of synaptic input across motoneuron pools may be a consequence of this. Specifically, this observation has been found in the plantarflexors during quiet standing (Vieira et al., 2012), unipedal standing perturbations (Cohen et al., 2020) and isometric contractions (Staudenmann et al., 2011). However, whether this organization persists during *voluntary postural* tasks is unknown. The purpose of this study is to determine if the spatial representations of motor unit action potentials in the plantarflexors are associated with force direction and contraction intensity during voluntary leaning. For this purpose, we observed muscle action potentials on a HDs-EMG by implementing a validated motor unit decomposition algorithm (Holobar et al., 2011). If plantarflexor motor units are recruited according to the location of their fibers, we would expect the action potentials of recruited motor units to be represented in muscle regions opposite to the direction of leaning to meet the force requirements of the task.

**Methods**

*Participants and Experimental Protocol*

 This study involved 14 healthy participants. Participants were excluded if they had any previous injury to their lower legs within the past 6 months, or any health conditions that negatively impacted balance (e.g., musculoskeletal disorders, concussion, stroke, etc.). The experimental protocol was approved by the institutional Ethics Committee and conformed to the latest amendment of the Declaration of Helsinki.

Participants were asked to stand in their natural bipedal stance on a piezoelectric force platform (9286AA Kistler, Zurich Switzerland). Individual center of pressure (CoP) targets at 5 different directions and centered at 60% and 80% of the limit of stability (LoS) were presented on a visual monitor in real-time (Figure 1A). Participants were instructed to lean towards each of the targets, maintain their CoP position in the target for 35 s, and then return back to their natural quiet stance. A rest period of 15s was provided between targets. An example of the CoP trace plot can be found in Figure 1B. To find the limit of stability, participants were instructed to lean about their ankles as far anteriorly, posteriorly, and laterally to both sides as they could without taking a step. This 4-way LoS test has been shown to be more reliable in testing LoS compared to other tests (**Thomsen** et al., 2017). After completing the 4-way LoS test, they performed a quiet stance trial for 30s.

The coordinate of the target locations ($t\_{COP\_{x}},t\_{COP\_{y}})$ were determined to reside over an ellipse representing the individuals’ LoS:

$$t\_{COP\_{x}}=k\_{LoS}b\cos(\left(\frac{π}{180}φ\right))+x\_{off}$$

$$t\_{COP\_{y}}=k\_{LoS}a\sin(\left(\frac{π}{180}φ\right))+y\_{off}$$

where $x\_{off}$ and $y\_{off}$ correspond to the average CoP position calculated during quiet standing. The semi axes (*a*) and (*b*) of the elliptic LoS were defined as the maximum CoP displacement in the anterior and lateral directions respectively from $y\_{off}$ and $x\_{off}$. The targets were displayed along this ellipse such that the distance between each starting position ($x\_{off},y\_{off}$) and the target locations was the same relative percentage of participant’s LoS. Five targets direction ($φ$) were calculated: 0° was directly lateral-right from the average CoP position in quiet stance and the 4 other targets deviated from this position moving 30° apart in an anti-clockwise direction (i.e. 30°, 60°, 90°, 120°) (Figure 1C). Targets were displayed as either a 60% LoS condition ($k\_{LoS}=60\%$) or 80% LoS condition ($k\_{LoS}=80\%$), with the order of target direction and LoS condition being randomized for each participant. This gave us two separate contraction intensities that were analyzed. A schematic of the targets with the two separate LoS conditions can be found in Figure 1C.

*High-Density Surface EMG Electrode Placement*

Placement of the HDs-EMG was guided using an ultrasound imaging system (LogicScan 64 LT-1T; Telemed, Vilnus, Lithuania). With participants lying prone and the ankle in the neutral position, the distal edges of the superficial aponeurosis of the MG and LG, the fascial space between the two muscles, the insertion of the MG and LG on the Achilles tendon, and the medial and lateral edges of gastrocnemius and SOL were identified and marked on the skin. Prior to grid placement, the skin was abraded and cleaned. One 32 channel semi-disposable grid with an interelectrode distance of 10mm (LISiN, Torino, Italy) was affixed to each of the MG and LG (one grid on each muscle). These grids were placed in the proximal region of the muscle, 10mm above the distal edges of the superficial aponeurosis of the MG and LG to avoid EMG detection from the distal region of gastrocnemius where EMG signals are known to propagate along the fibres (Gallina et al., 2013a). Two adjacent 32 channel semi-disposable grids with an interelectrode distance of 10mm (LISiN, Torino, Italy) were placed over the SOL muscle creating a single matrix of 64 channels. The 64 channeled-grid was centered on the Achilles tendon and placed 10mm below the distal insertion of the MG. The grids were held in place using bio-adhesive foam, and conductive paste ensure optimal contact between the skin and the electrodes (Figure 1D). Three reference electrodes were placed on the patella (MG), the fibular head (LG), and the medial malleolus (SOL).

*HDs-EMG and Forceplate Recordings*

Signals were detected in monopolar configuration using a novel modular and wireless HDs-EMG amplifier (Cerone et al., 2019). This device is composed of four modules (one for each gastrocnemius head, and two for SOL), each detecting, conditioning, and transmitting 32 EMG signals (Gain: 192V/V; sampling frequency: 2048 Hz; 16-bit A/D Converter). A Wi-Fi link from the modules to a personal computer enables the detected signals to be recorded, visualized and stored in real-time.

CoP coordinates in the sagittal and frontal planes were computed from the ground reaction forces recorded by a piezoelectric force platform (9286AA Kistler, Zurich, Switzerland). Ground reaction forces were sampled at 2048 Hz using a 16-bit A/D Converter (±2.5 V input dynamic range). A pulse generator (LISiN, Torino, Italy) sent a signal at 3Hz to both EMG amplifier and force platform to use for synchronization of both systems.

**Data Analysis**

All EMG data analyses were performed using MATLAB R2020a (The MathWorks, Inc., Natick, MA, USA). Single-differential EMGs between pairs of adjacent electrodes along each column of the matrix were computed from the monopolar signals and inspected for quality. High-quality signals were evaluated based on the visual identification of channels. Channels presenting contact problems or power line interference were linearly interpolated with the data collected from up to the closest 4 channels surrounding it. After verifying the quality of all EMG signals, monopolar signals were filtered (Butterworth, 2nd order, 20-350 Hz) and decomposed (Holobar et al., 2011) separately for each target direction and LoS condition. After decomposition of the EMG signals, the firing instants of identified motor units were used to trigger and average single differential EMGs over 30 ms epochs, providing the surface representation of single motor unit action potentials (Farina et al., 2002).

The results of the decomposition were inspected for spurious units. Visual analysis was conducted on all of the extracted signals and non-physiological potentials (i.e., propagating potentials or noisy waveforms) were discarded. Examples of retained motor units is shown in Figure 2.

A motor unit tracking analysis was conducted. Motor unit action potentials that were common between the different leaning directions (performed separately for the 60% and 80% LoS conditions) were identified. The two sets of action potentials for each pair of motor units were aligned in time by maximizing their cross-correlation function. The mean square difference was computed between the two sets of time-aligned action potentials, averaged across channels, then normalized with respect to the mean ARV of the two sets of action potentials. Finally, pairs of motor unit action potentials with a mean square difference smaller than 5% were considered common (Farina et al., 2008). This provided us with a group of motor units that will be referred to as ‘common units’ and a group of motor units not paired which will be called ‘unique units’ from this point.

For each retained motor unit, the ARV was calculated across 30 ms epoch centered on individual action potentials. The maximum ARV value was calculated along both the column and the rows of the grids, providing the surface distribution of the motor unit action potential amplitude across both medio-lateral and proximo-distal directions. To improve the accuracy of spatial distribution measures, muscle activity in MG, LG, SOL was quantified from the cluster of channels with amplitude above 70% of the ARV of the channels with the highest activity for each muscle (Vieira et al., 2010). The location of the peak activity was calculated as:

$$Barycenter= \frac{∑ARV\_{ch}POS\_{ch}}{∑ARV\_{ch}}$$

With ‘ch’ being each channel in the cluster of channels with amplitude above 70% of the ARV, and ‘POS’ being their position along either rows (medio-lateral) or columns (proximo-distal) on the electrode matrix. The barycenter is the location on the muscle where the motor unit action potentials are more clearly represented. The barycenter position was averaged for motor units separately for each direction, and LoS condition, and considered for analysis.

 The number of channels with an amplitude above 70% ARV for the barycenter calculation was computed. This value represents the area of muscle fibers being activated for a specific motor unit and can be considered an indirect indicator of the physiological size (innervation ratio) of the motor unit. This value is referred to as the size of the motor unit from this point.

**Statistical Analysis**

Statistical analyses were conducted using SPSS v.26 (IBM Corp, Armonk, NY). Barycenter values and the size of the motor units were not normally distributed, as assessed by Shapiro-Wilk’s test (*p* < 0.05). Distributions of barycenter locations and the size of the motor units were similar for all groups, as assessed by visual inspection of boxplots. To determine surface spatial differences on the plantarflexor muscles, the medio-lateral (X) and proximo-distal (Y) coordinates of the barycenter from the decomposed motor units in the MG, LG and SOL across the different target directions and LoS conditions were compared using separate Kruskal-Wallis H Tests. When a significant main effect was found, pairwise comparisons were performed using Dunn’s (1964) procedure with a Bonferroni correction for multiple comparisons (asymptotic (2-sided tests), level of significance *p* < .0125). Adjusted p-values are presented. The 0° condition was compared to the other target directions (30°, 60°, 90°, 120°). The 0° comparator was chosen as it portrays the largest change in directional force requirement. Similar results were found using the 120° condition as the comparator. The statistical analysis was conducted for the two groups of motor units (common and unique units) to determine whether the two groups of motor units displayed spatial differences. To determine if the two groups of motor units had different sizes, multiple Mann-Whitney U tests with Bonferroni corrections for multiple comparisons (asymptotic (2-sided tests), level *p* < .01) were conducted between target directions.

**Results**

The total number of identified motor units for each muscle and LoS condition can be found in Table 1. The number of motor units identified for each target direction can be found in Figure 3.

The multi-directional leaning task revealed a significant shift in the location of the barycenter within the plantarflexor muscles; the barycenter locations shifted medially and proximally as the leaning direction changed from 0° to 120°. The median barycenter values in the medio-lateral direction (X-coordinate) were significantly different between leaning target directions for the SOL (60%:$ χ^{2}$(4) = 10.335, *p* = 0.035; 80%: $χ^{2}$(4) = 16.267, *p* = 0.003) and MG (60%:$ χ^{2}$(4) = 14.803, *p* = 0.005), but not for LG (*p* > .05). For the post-hoc analyses, review Figure 3. The median barycenter values in the proximo-distal direction (Y-coordinate) were significantly different across the leaning target directions for the SOL (60%: $χ^{2}$(4) = 10.335, *p* = 0.035) and MG (80%: $χ^{2}$(4) = 9.327, *p* = 0.05), but not for the LG (*p* > 0.05). For the post-hoc analyses, review Figure 3.

The group totals for the barycenter values did not fully address our hypothesis of determining an association between barycenter location and leaning direction. Accordingly, we decided to analyze the motor units as separate groups (common and unique units) and conduct separate statistical analyses on these groups. Once separated, a clear difference between the groups was illustrated. Kruskal-Wallis H Test’s determined that there were statistical differences in the median medio-lateral and proximo-distal barycenter values for the unique units (*p* < .05) across target directions but not for the common units (*p* > .05), suggesting that the unique units exhibit spatial positional changes whereas the common units do not (Figure 4, 5). In addition, the size of the unique units was significantly larger than the common units (*p <* 0.05) (Table 2).

The median barycenter values in the medio-lateral (X-coordinate) direction were significantly different across the leaning target directions for the MG (60%: $χ^{2}$(4) = 9.694, *p* = 0.046) and SOL (60%: $χ^{2}$(4) = 13.343, *p* = 0.01; 80%: $χ^{2}$(4) = 14.093, *p* = 0.007) but not for the LG (*p* > 0.05). For the post-hoc analyses, review significant differences in Figure 4 (MG) and Figure 5 (SOL). The median barycenter values in the proximo-distal (Y-coordinate) direction were significantly different across the leaning directions for the MG (80%: $χ^{2}$(4) = 10.744, *p* = 0.03), (SOL (80%: $χ^{2}$(4) = 18.899, *p* = 0.01), but not for the LG (*p* > 0.05). For the post-hoc analyses, review significant differences in Figure 4 (MG) and Figure 5 (SOL).

The multi-directional leaning task also revealed a significant effect on the size of the motor units being recruited. As the target directions shifted counterclockwise, the size of the motor units increased for the MG (60%: $χ^{2}$(4) = 31.08, *p* < 0.001; 80%: $χ^{2}$(4) = 43.787, *p* <0.01), LG (80%: $χ^{2}$(4) = 34.511, *p* < 0.001), and SOL (80%: $χ^{2}$(4) = 16.421, *p* = 0.003) suggesting more muscle fibers being activated in these target directions. Post-hoc analyses revealed the size of the unique units were significantly larger than the common units for the MG (*p* < 0.001), LG (*p* < 0.001), and SOL (*p* < 0.001), between the 30°, 60°, 90° target directions (Table 2).

**Discussion**

HDs-EMGs were recorded from the three ankle plantarflexor muscles to address the question of whether voluntary leaning in multi-directions and contraction intensity has an effect on the spatial representations of motor units. Our findings illustrate that leaning directions has an effect on the location of the spatial representations of motor units in the MG and SOL. This localized activity is illustrated to a further extent when separating the motor units into groups of common and unique units. The unique units appeared to have spatial differences associated with the different target directions, whereas the common units appeared to remain in a constant spatial location. The size of the unique units was also significantly smaller than the common units. Contraction intensity had a variable effect on the spatial representations of motor units. However, spatial representations were found to shift in the proximo-distal (MG, SOL) and medio-lateral (SOL) directions for the larger contraction intensities (80% LoS), specifically for the unique units. This may suggest that the CNS has the capability of activating two separate groups of motor units to modulate force requirements during voluntary activation of the plantarflexor muscles.

*Regional recruitment of plantarflexor motor units*

During the leaning task, the shifts in the spatial representation of the motor units on the HDs-EMG grids appeared to be accounted for by the recruitment of different (unique) motor units in localized regions. This observation is consistent with our previous work and supporting studies (Cohen et al., 2020, Vieira et al., 2011, Hodson-Tole et al., 2012). Previously, we observed a task-dependent modulation of the ankle plantarflexors in response to perturbations in different directions using global measures of EMG (Cohen et al., 2020). While we speculated that this modulation was the result of task-specific motor unit recruitment, the brief episodic nature of the perturbations in that study did not allow us to decompose motor units. In our present study, in which participants sustained a voluntary lean in different directions, we were able to confirm that motor units are recruited in accordance with the direction-specific force requirements of the task. Motor unit spatial representations shifted opposite to the direction of the target direction in the MG and SOL. Vieira et al., (2011) observed that motor units in the medial gastrocnemius are spatially localized in the proximal-distal plane during quiet standing, which may be utilized by the CNS to activate sub-volumes of the muscle. It appears from our data that the localization of the motor units in this plane continues during voluntary activation of the plantarflexors as motor units were recruited in the proximal regions of the muscles as the target directions moved counterclockwise and with increasing contraction intensity (Figures 3, 4, 5). Hodson-Tole et al., (2012) illustrated that during a task of standing in which no swaying occurs (participants fixed to a board), the activated motor units tended to be represented in the distal regions. The motor units identified in the distal region of the grid may very well be recruited for quiet standing, but once contraction intensity increases, with increasing task difficulty (60% to 80% of LoS), recruitment of new motor units in the proximal regions occur as found in our study. In agreement with Hodson-Tole et al., (2012), during the less force-demanding task at 0° target direction, the barycenter values for the motor units were localized near the distal portions of the muscles (Figures 3, 4, 5).

Interestingly, when analyzing the difference between common and unique motor units, we found that the motor units that are common across the target directions, as expected, did not have different spatial locations (Figure 4, 5). This unique pattern exhibited in our study provides a different model for spatial localization during voluntary leaning tasks. Rather than the CNS simply recruiting units in different spatial locations according to their mechanical advantage (see below), it appears that there may be a nuanced activation pattern being utilized. Specific common motor units are recruited for a ‘baseline’ force modulation, and the CNS recruits new unique units in different spatial locations to augment the force requirements. If this is the case, we would expect the common units to be smaller (recruited first) compared to the unique units. Our results provide indirect evidence of this. The size of the unique units was significantly larger than the size of the common units (Table 2). This suggests that the common motor units innervate less muscle fibers and would be recruited first according to Henneman size principle (Henneman et al., 1965; Brown-Milne et al., 1976). Strikingly, the number of common units during the 60% and 80% LoS conditions remains relatively constant (average increase of 11 motor units), whereas the increase in motor units for the 80% LoS condition appears to be accounted for by the unique units (average increase of 130 motor units) (Table 1). This provides further evidence that once task demands exceed the ability of the common units to modulate the force, the CNS recruits the unique units.

Contraction intensity seemed to have a relatively variable effect on the spatial representation of the motor units. Previous studies have observed that contraction intensity can affect the spatial localization of global EMG root mean square values (RMS) (Gallina et al., 2013b; Watanabe et al., 2013), however, observed results are relatively variable as well. For example, Gallina et al., (2013b) noticed that the location of a global barycentre was significantly dependent on the subject within the trapezius muscle. Watanabe et al., 2013 investigated surface manifestations of activity on the rectus femoris. The group found that during isometric contractions of knee extension and hip flexion, normalized RMS values tended to increase without a considerable region-specific pattern for hip flexion, whereas knee extension tended to increase RMS activity in the proximal and distal regions. Consequently in our study, the contraction intensity appears to have some effect on altering the spatial location of the motor units, however the results are variable. The regional recruitment of motor units might therefore respond more to directionality information rather than contraction intensity.

*Functional implications*

While the leaning task had an effect on the MG and SOL, the hypothesis that the LG motor units’ spatial representations are associated with target directions was not accepted. The leaning task itself requires participants to not only plantarflex, but also puts the ankle into relative inversion, requiring eversion torques to remain upright and standing. While conventionally thought to exclusively plantarflex, the ankle plantarflexors appear to be involved during inversion and eversion torques. Previous studies (Lee and Piazza 2008, Vieira et al., 2013) have observed that inversion-eversion torques derive from the gastrocnemius muscles. More specifically, during relative ankle-joint inversion, the inversion moment arm increases for the LG (Lee and Piazza 2008). As a result of the leaning task causing the ankle joint to increase its relative inversion, it may have exceeded the LG capabilities to produce an eversion torque. Therefore, the directional force requirements for the LG may indeed require a neutral ankle joint in order for the CNS to recruit motor units from separate locations. On the other hand, it appears that during this relative ankle inversion the CNS is able to recruit motor units from separate locations in the MG and SOL. It is assumed that there is still a large enough eversion moment arm in these muscles to produce the torque required to maintain upright standing and utilize the directionality information.

When evaluating the number of motor units decomposed in each target direction, the LG had the least number of units decomposed (Figure 3). This may suggest that leaning in these directions may result in greater compensation from the left leg to modulate the force rather than utilization of the LG muscle. Indeed, the LG muscle is quite smaller compared to the MG muscle. It is therefore possible that the force requirements during bipedal standing may limit the LG’s ability to modulate force and the MG muscle on the left leg will take control of the force requirements.

*Potential Mechanisms*

In this study, we provide evidence of recruitment of motor units in separate spatial locations. This observation is likely associated with the previously observed non-homogenous activation of the ankle plantarflexors during a variety of tasks (Segal and Song 2005, Kinugasa et al., 2011, Staudenmann et al., 2009, Cohen et al., 2020). Each of these studies describe the ankle plantarflexors activating in regionally specific areas in association with force direction (Staudenmann et al., 2009; Cohen et al., 2020), or with contraction intensity (Segal and Song, 2005, Kinugasa et al., 2011). The underlying assumption in these studies is that localized motor units are recruited based on their mechanical advantage. Our results provide a confirmation that motor units in localized regions are recruited based on task demands; specifically, directionality of the task demands.

In order to support the control of different motor units within a muscle it has been proposed that muscles that perform different types of kinematic tasks may be functionally demarcated into task-oriented groups of motor units, or ‘task groups’ (Loeb 1985). These task groups may have intrinsic properties optimized for the performance of a specific functional task (Hoffer et al., 1987), however recent studies suggest that the physical location of the units may be important (Hodson-Tole et al., 2009). Seeing that individual muscles are nonuniform with their mechanical actions (Chanaud et al., 1991), directional tuning of single motor units have been observed (Hermann and Flanders, 1998). The directional tuning of single motor units seems to depend more upon the location of motor units within the muscle volume rather than on the degree of muscle activation (Herrmann and Flanders, 1998). Since the location of motor units is influential, the idea that motor units are recruited based on mechanical advantage has been further explored (Hodson-Tole et al., 2009). Indeed, motor units situated in optimal positions to create torques are preferentially recruited (Butler and Gandevia 2008). Butler and Gandevia (2008) classified this observation as the neuromechanical principle by which the CNS controls motoneuronal recruitment. While Butler and Gandevia (2008) findings were modeled in the human respiratory muscles, other authors have found similar results in the ankle plantarflexors (Heroux et al., (2014) and Cohen et al., (2020)). Our results demonstrate that the motor units opposite to the direction of the target angles would most likely be situated for more effective generation of ankle plantar-flexion and eversion torque during the voluntary leaning task. We therefore suggest that the unique motor units in the MG and SOL are in the optimal location to effectively contribute to the torque requirements during the leaning task. The distinction between common and unique units adds an additional layer to this hypothesis. Common units, by definition, did not show changes in spatial representation to force directions and therefore may be recruited to create a basic plantarflexion torque. Once common motor units are recruited, the CNS recruits the unique units in optimal locations, in addition to the size of the units, in order for successful postural control. It should be noted that this hypothesis differs slightly from Hermann and Flanders (1998) interpretation of motor units being sequentially recruited and derecruited based on direction. A key consideration between this difference is in the assessment of the plantarflexors rather than the biceps brachialis. Any group of muscles can act as postural muscles depending on the body parts in contact with the environment and the biomechanical requirements of equilibrium (Macpherson et al., 1989). However, the plantarflexor muscles in our study would be considered postural muscles, whereas the task required of the bicep brachialis in Hermann and Flanders (1998) experiment would not consider them as postural muscles. Therefore, there may be different recruitment strategies for the different postural and non-postural tasks that the CNS can exploit.

*Possible Limitations*

The location of the fibers of excited motor unit is the most likely explanation to the regional differences in the spatial representations of the motor unit action potentials. However, differences between leg lengths, muscle lengths, and the EMG to skin interface may confound some of these differences. Nevertheless, exceptional care was taken in the placement of the electrodes (see ultrasound procedure in methods), and we believe that these confounders have a minor influence on our findings. Further, as stated above the force-requirement of the LG may not have precluded the possibility for it to exhibit regional differences as the muscles action was not situated to allow for recruitment of units in different locations. As a result, interpretations of our data for the LG should be made with caution.

**Conclusion**

This study supports regional recruitment of motor units in the MG and SOL, but not the LG during a voluntary multi-directional leaning task. This recruitment pattern was related to leaning direction, with motor units recruited medially and proximally in the MG and SOL as the target directions moved in an anti-clockwise direction. This reveals a task-dependent recruitment of the motor units in the MG and SOL during voluntary leaning. The recruitment is dependent on the directionality of the force-requirements, and the CNS may be utilizing this information to modulate the appropriate force.

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