

Synchronization of Motor Units in Human Soleus Muscle During Standing Postural Tasks

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Mochizuki, G., T. D. Ivanova, and S. J. Garland. Synchronization of motor units in human soleus muscle during standing postural tasks. *J Neurophysiol* 94: 62–69, 2005; doi:10.1152/jn.01322.2004. During standing posture, the soleus muscles act to control sway in the anteroposterior (AP) direction. The soleus muscles bilaterally share a common function during standing tasks. We sought to determine whether common descending inputs, as evidenced by the synchronization of bilateral motor unit pairs, were employed as a strategy to control this common function. Single motor units were recorded from the soleus muscles in subjects who stood on adjacent force platforms for 5 min with their eyes open or closed. While standing with the eyes open, only 4/39 bilateral motor unit pairs showed significant synchronization. Similarly, only 3/36 motor unit pairs were significantly synchronized during the eyes closed task. The low incidence of synchronization was observed despite a high correlation in the amount of sway in the AP direction between legs in both the eyes open and eyes closed tasks ($\rho = 0.80$ and $\rho = 0.83$, respectively). When the extent of synchronization was assessed between pairs of motor units within the same leg with the eyes open, 10/12 pairs were synchronized. Furthermore, when pairs of soleus motor units were recorded both bilaterally and unilaterally during voluntary isometric ankle plantarflexion, only 4/30 bilateral pairs showed significant synchronization, whereas 19/24 unilateral pairs had significant synchronization. In this study, there was little evidence of the existence of synchronization between bilateral soleus motor unit pairs in either postural tasks or voluntary isometric contractions. In cases in which bilateral synchronization was observed, it was considerably weaker than the synchronization of motor units within a single soleus muscle. The results of this study reveal that it is rather uncommon for bilateral soleus motoneurons to receive common descending synaptic inputs, whereas two motoneurons within a single soleus muscle do.

INTRODUCTION

During muscle contractions, motoneurons will sometimes produce synchronous discharges. Motor unit synchronization is observed when two distinct motor units fire at the same time or within a few milliseconds of each other more often than is due to chance (Sears and Stagg 1976). Synchronization can be categorized into two groups, depending on the width of the peak of the cross-correlation histogram. Short-term synchronization is characterized by a narrow (approximately ± 5 ms), centrally located peak in the cross-correlation histogram of two concurrently active motor units and is believed to reflect the simultaneous arrival of distinct unitary excitatory postsynaptic potentials (EPSPs) to the motoneuron pool as a result of last-order branching of corticospinal inputs (Sears and Stagg

1976). On the other hand, broad-peak synchronization is identified by a centrally located peak in the cross-correlation histogram that is broader (approximately ± 20 ms) and of lower amplitude. It is thought that the wider peak is illustrative of presynaptic synchronization of separate sources at the spinal or supraspinal level (Kirkwood et al. 1982).

Synchronization has been observed between motor units within hand or forearm muscles during isometric muscle contractions (Bremner et al. 1991; Datta and Stephens 1990; Keen and Fuglevand 2004; Schmied et al. 1993, 2000; Semmler and Nordstrom 1998), anisometric contractions (Semmler et al. 2002), and conditions of altered proprioceptive inputs (Garland and Miles 1997). In the lower limb, synchronization has been shown to be present in the tibialis anterior muscle during gait (Halliday et al. 2003; Hansen et al. 2001) and during isometric contractions (Datta et al. 1991; Nielsen and Kagamihara 1994). Nielsen and Kagamihara (1994) also showed synchronization within the soleus muscle during an isometric contraction. In addition, synchronization has been observed across the soleus and gastrocnemius (Dietz et al. 1976; Halliday et al. 2003; Hansen et al. 2001) and the soleus and tibialis anterior (Nielsen and Kagamihara 1994) during gait and isometric contractions. However, very little work has been done to study motor unit synchronization in the lower limb during standing postural tasks. To our knowledge, only Gibbs et al. (1995) have reported evidence of synchronization between bilateral gastrocnemius muscles in subjects during quiet standing and during a demanding balancing task. In that case, the bilateral gastrocnemius muscles were thought to act together to share a common function. Such commonality in function has been shown to be attributable to bilateral synchronization in the diaphragm, rectus abdominis, and masseter muscles as well (Carr et al. 1994).

The control of quiet stance is a task that requires bilateral activation of the ankle plantar flexors according to the “inverted pendulum” model of standing posture (Winter et al. 1998). In this model, the CNS adjusts the center of pressure (COP), which is the neurophysiological response to changes in the body’s center of mass (COM) (Winter 1990), to maintain upright stance. Both soleus (Masani et al. 2003) and gastrocnemius (Gatev et al. 1999; Masani et al. 2003) muscle activity has been shown to be correlated to excursions of the COP. However, the soleus muscle may play a predominant role in adjusting the COP to match changes in the COM in quiet stance because the gastrocnemius has been shown to be less

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active than the soleus during standing posture in humans (Duysens et al. 1991) and in cats (Hodgson 1983). The dominant role of the soleus over the gastrocnemius in quiet stance may be related to muscle fiber type, with ~80% of the soleus being comprised of type I muscle fibers compared with 57% in the gastrocnemius (Gollnick et al. 1974).

When the feet are placed side-by-side during bipedal stance, the anteroposterior (AP) center of pressure displacement of each leg has been shown to be similar during quiet standing (Winter et al. 1993) and during bilateral shoulder flexion movements (Mochizuki et al. 2004a). Additionally, Winter et al. (1996) have revealed that, in this standing position, the motor control strategies that preside over AP sway and medio-lateral (ML) sway are independent. That is to say that ankle plantarflexors are responsible for the AP component of sway, whereas the hip abductors/adductors control ML sway. The amount of both AP and ML sway has been shown to increase when the eyes are closed (Lucy and Hayes 1985). Furthermore, Winter et al. (1993) have shown that the correlation of sway between the contact forces of the two feet increases in both the AP and ML directions when the eyes are closed, possibly reflecting an increase in synchronization of motor unit activity.

Given that the displacement of the center of pressure of each foot is symmetrical during quiet stance, it is likely that the ankle plantarflexors (bilaterally) work in unison to control postural sway. One mechanism through which this control could be exerted bilaterally is motor unit synchronization. Therefore the purpose of this study was to determine whether bilateral soleus motor units would exhibit synchronized firing behavior during standing postural tasks. It was hypothesized that synchronization of bilateral soleus motor units during postural tasks would be observed and would be more evident when the eyes were closed than when the eyes were open. Portions of these results have been reported previously in abstract form (Mochizuki et al. 2004b).

METHODS

Subjects

Eleven subjects (8 males and 3 females; height, 173.6 ± 12.4 cm; weight, 74.9 ± 15.9 kg; age, 28.0 ± 6.4 yr) with no known neuromuscular disorders participated in the study after providing informed written consent. This study was approved by the Review Board for Health Sciences Research Involving Human Subjects at the University of Western Ontario and conformed to the standards established by the Declaration of Helsinki.

Experimental procedure

Subjects stood barefoot with their feet shoulder width apart and with each foot on adjacent AMTI ORG-6 force platforms (Advanced Mechanical Technology, Watertown, MA). With the head looking straight ahead and with the arms hanging loosely at their sides, subjects performed two 5- to 10-min trials (eyes open or eyes closed) of quiet standing, which were separated by a 5-min rest period. The order of the trials was randomly assigned.

A subset of subjects also performed submaximal voluntary isometric contractions for 5 min. These contractions were performed in sitting with the hip and knees at 90° as the subjects plantarflexed against a light resistive load applied just proximal to the knee.

Data acquisition

FORCE PLATFORM MEASURES. All signals were digitized on-line using a 16-bit acquisition system (Power 1401 with Spike2 software, Cambridge Electronic Design, Cambridge, UK). All data were stored on an IBM Pentium III laptop computer (International Business Machines, Armonk, NY) for off-line analysis. The signals from the force platforms were sampled at 100 Hz and saved for off-line computation and analysis of the COP displacements in the AP and ML directions.

MOTOR UNIT RECORDINGS. Single motor unit potentials were recorded intramuscularly using fine wire bipolar electrodes (California Fine Wire, Grover Beach, CA). Each electrode was comprised of three Formvar-insulated, $50\text{-}\mu\text{m}$ -diam stainless steel wires, fastened together at the recording tip with cyanoacrylate adhesive. The electrode was threaded through a disposable 2-cm-long, 25-gauge hypodermic needle (Becton Dickinson and Company, Franklin Lakes, NJ), with a hook of ~2 mm in length formed at the recording end of the electrode. The needle was used to insert the electrode and then was withdrawn, leaving the wire embedded within the muscle. All wire electrode-hypodermic needle pairings were sealed and autoclaved prior to use (AMSCO Autoclave). The electrodes were inserted into the lateral aspect of the soleus muscle bilaterally at approximately the same position.

The motor unit recordings were amplified, filtered (90 Hz to 10 kHz), and sampled at 25 kHz. Off-line motor unit discrimination was accomplished using a template-matching algorithm (Spike2) that classified motor units according to their amplitude and shape. Care was taken to ensure that identified motor unit action potentials were associated with the same motor unit. Any sections of data where motor unit action potentials could not be classified with 100% certainty were excluded from subsequent analysis.

SURFACE EMG. Bipolar Ag-AgCl electrodes (2-cm interelectrode distance) were used to record the surface EMG from the soleus (SOL), medial gastrocnemius (MG), and tibialis anterior (TA) muscles. The surface EMG signals were amplified, filtered (10–1,000 Hz), sampled at 2,500 Hz, and saved for off-line analysis.

Data analysis

COP. The COP displacement was first determined in the sagittal and frontal planes according to the following equations for AP sway and ML sway, respectively

$$\text{COP}_{\text{AP}} = M_x/F_z \quad (1)$$

$$\text{COP}_{\text{ML}} = -M_y/F_z \quad (2)$$

where M_x and M_y are the force platform measures of the moment of force, and F_z is the vertical ground reaction force. To consider only the fluctuations in COP excursions, the DC component of the signal was removed using a built-in function in Spike2 with a time constant of 0.75 s. This had the same effect as applying a high-pass filter with a -3-dB point of 0.5 Hz.

The cross-correlation functions were derived by correlating, on a point-by-point basis, the two platform measures of both AP and ML sway. The cross-correlation coefficient (ρ) was taken as the peak in the function within ± 1.0 s of time 0 with a value between -1.0 (perfect negative correlation) and 1.0 (perfect positive correlation). This analysis was only performed over sections of data during which both motor units were tonically active. The correlation function was applied to the COP excursions during both the eyes open and eyes closed tasks.

The amount of sway in the AP and ML directions was determined by assessing the SD of sway (SDSWAY) of the original signal for the sections of data during which both motor units were tonically active.

This analysis was performed on the COP signals from both force platforms for both tasks.

SYNCHRONIZATION. Cross-correlation histograms were computed to assess synchronization between motor unit spike trains. The histograms were constructed using a minimum of 1,800 spikes from each spike train. The train with the greatest number of spikes was used as the trigger (Schmied et al. 2000). Histograms were comprised of bins over a range of ± 50 ms, with each bin having a width of 0.25 ms. The presence of peaks in the histogram was verified using the cumulative sum technique (CUSUM; Ellaway 1978), which involved subtracting the mean baseline value (taken over the bins from -50 to -10 ms) from the number of counts for each bin, and cumulatively summing each resultant. In the cases in which no peaks were observed, the analyzed region comprised the bins over the central 20 ms (-10 to 10 ms) of the histogram (Schmied et al. 2000). The strength of synchronization was quantified using the k' value, which is a ratio of the number of counts in the peak to the number of counts in the baseline value within the peak (Ellaway and Murthy 1985). As a second measure of the strength of synchronization, the strength of common input (CIS) was calculated. This measure of the frequency of synchronization (i.e., the number of extra counts in the peak divided by the duration of the trial) has the benefit of not being influenced by motor unit firing rate (Nordstrom et al. 1992). The significance of the histogram peak was determined using $P < 0.001$, according to the method of Wiegner and Wierzbicka (1987).

Statistical analysis

Statistical analysis was performed using SPSS v11.0 (SPSS, Chicago, IL). Platform-to-platform cross-correlation coefficients (ρ), SD-SWAY (AP and ML of each leg), and k' and CIS of bilateral motor unit pairs were compared between postural tasks (eyes open vs. eyes closed) using independent t -tests. Kolmogorov-Smirnov and Levene tests were used to assess the normality of distribution and homogeneity of variance for all analyzed data. For motor unit pairs showing significant synchronization, the tests showed that neither the k' nor CIS values met the criteria to use parametric statistics. As a result, nonparametric Mann-Whitney U -tests were used to assess the differences in the magnitude of synchronization across conditions. All values are reported as means \pm SD. Statistical significance was set at $P < 0.05$.

RESULTS

Synchronization in bilateral soleus

In total, 39 motor unit pairs were analyzed for evidence of synchronization during the eyes open task. Only 4/39 pairs of motor units showed significant synchronization. Quantification of all motor unit pairs revealed a mean k' of 1.03 ± 0.08 and

a mean CIS of 0.02 ± 0.07 . The extent of synchronization for the four significant peaks was $k' = 1.22 \pm 0.06$ and CIS = 0.18 ± 0.06 . The mean width of the significant peaks was 20.6 ± 3.0 ms. Figure 1, A and B, shows the histogram and CUSUM for two different subjects revealing nonsignificant (A) and significant (B) synchronization between motor units.

The extent of synchronization was assessed in 36 pairs of motor units during the eyes closed task, with only 3/36 pairs revealing significant peaks in the cross-correlation histogram. Eighteen of these pairs were also recorded during the eyes open trials; these motor unit pairs did not show significant synchronization in either task. The mean k' and CIS for all pairs were 1.04 ± 0.07 and 0.03 ± 0.07 , respectively. For the three pairs of motor units with significant synchronization, the k' and CIS were 1.17 ± 0.02 and 0.09 ± 0.03 , respectively. The mean width of the peak for these trials was 16.5 ± 3.5 ms. Neither the k' nor the CIS values differed between the eyes open and eyes closed tasks. Figure 1C shows the histogram and CUSUM for a different subject in the eyes closed condition in which no significant peak was observed.

Synchronization in unilateral soleus

Given that there are fewer direct corticospinal projections to the soleus muscle compared with upper limb (Brouwer and Ashby 1990) and other lower limb muscles (Brouwer and Ashby 1992) and the paucity of information in the literature regarding synchronization during standing postural tasks, it was important to determine whether the soleus motor units within a single muscle would exhibit synchronization. Thus motor unit pairs within a soleus muscle were assessed during the postural tasks in six subjects. The procedures for recording pairs of unilateral motor units were identical to that of the bilateral recordings except that both intramuscular electrodes were inserted 2–3 cm apart into a single, randomly chosen, soleus muscle. From the six subjects tested, 10/12 motor unit pairs revealed significant synchronization during the eyes open task. For these 10 significant pairs, $k' = 1.46 \pm 0.11$ and CIS = 0.34 ± 0.19 and the width of the peak was 13.5 ± 3.7 ms. Figure 2A shows the histogram and CUSUM of a subject showing synchronization between unilateral motor units. Four pairs of motor units were recorded unilaterally and analyzed during the eyes closed task. All of the four pairs revealed significant synchronization, with $k' = 1.47 \pm 0.24$, CIS = 0.25 ± 0.08 , and width = 11.8 ± 4.4 ms (see Fig. 2B). Three of these pairs also were recorded during the eyes open task and

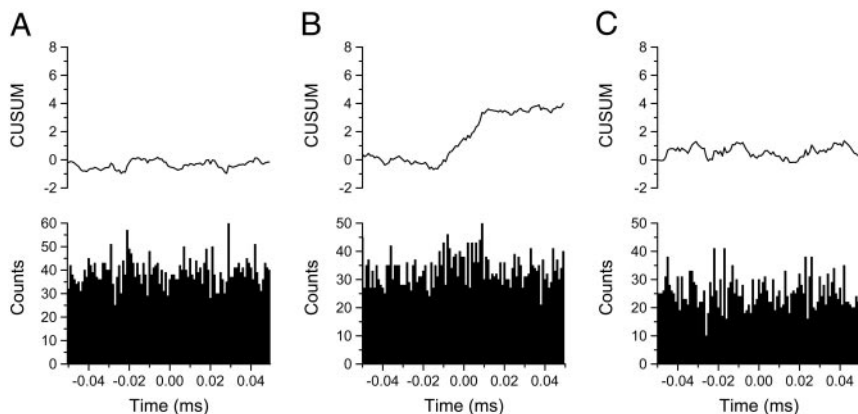


FIG. 1. Cross-correlation histograms and normalized cumulative sum (CUSUMs) for bilateral motor unit pairs from 3 different subjects. A: absence of synchronization between soleus motor units in the eyes open postural task. B: significant synchronization between bilateral soleus motor units in the eyes open postural task. C: no significant synchronization between motor units in the eyes closed postural task. CUSUMs are normalized to mean baseline value. Bin widths in the histograms are 1 ms (used only for illustrative purposes).

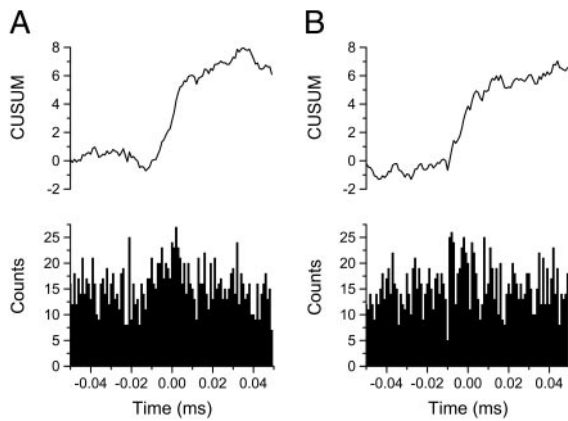


FIG. 2. Cross-correlation histograms and normalized CUSUMs for unilateral motor unit pairs showing significant synchronization in the eyes open (A) and eyes closed (B) postural tasks. Data are from the same subject. CUSUMs are normalized to mean baseline value. Bin width in the histograms is 1 ms (used only for illustrative purposes).

produced significant histogram peaks ($k' = 1.46 \pm 0.07$, CIS = 0.25 ± 0.01 , and width = 12.4 ± 2.2 ms).

Synchronization during voluntary isometric contractions

The extent of synchronization observed during postural tasks was compared with that observed during a voluntary isometric contraction. Unilateral and bilateral soleus motor unit activity was recorded with two intramuscular electrodes in each muscle in four of the subjects while they performed isometric contractions of the ankle plantarflexors against a light resistive force. The incidence and extent of synchronization observed during voluntary isometric contractions were similar to that found during the postural tasks. Bilateral recordings revealed that only 4/30 motor unit pairs showed synchronous firing. For the significant pairs, $k' = 1.24 \pm 0.05$, CIS = 0.12 ± 0.02 , and width = 14.7 ± 3.9 ms. In unilateral recordings, 19/24 motor unit pairs had significant synchronization. The k' , CIS, and peak width for the 19 significant pairs was 1.50 ± 0.22 , 0.31 ± 0.13 , and 15.6 ± 3.8 , respectively. Figure 3 shows the mean k' and CIS values for significant motor unit pairs across conditions. Unilateral motor unit pairs had significantly larger indi-

ces of synchronization than bilateral motor unit pairs regardless of whether the task was a voluntary isometric contraction or a postural task ($P < 0.03$). There was no significant difference between tasks (postural vs. isometric contraction).

For both the postural task and voluntary isometric contraction, the distributions of k' and CIS scores for all motor unit pairs (nonsignificant, bilateral significant, and unilateral significant) revealed that both the k' and CIS values of the nonsignificant pairs were lower than the bilateral significant pairs, which in turn, were lower than the unilateral significant pairs. The distributions of k' and CIS values for the eyes open postural task and voluntary isometric contraction are depicted in Figure 4.

Force platform measures

The cross-correlation analysis of the AP sway revealed strong relationships in the sway characteristics between legs. In the eyes open task, $\rho = 0.80 \pm 0.09$, and in the eyes closed task, $\rho = 0.83 \pm 0.06$. The peak of the cross-correlation function occurred at -1.4 ± 19.0 ms, with respect to *time 0*, for the eyes open trials and -3.8 ± 17.8 ms for the eyes closed trials. Combined, these values indicate that in both tasks, the oscillations in sway between legs were tightly coupled with virtually no time lag between legs. Analysis of the correlation of ML sway between legs revealed moderate negative correlations ($\rho = -0.64 \pm 0.20$, eyes open; $\rho = -0.70 \pm 0.17$, eyes closed). There were no differences in the cross-correlation coefficient in either AP or ML sway between tasks. In addition, there was no difference in the amount of sway between tasks in either the AP or ML direction (Table 1). Figure 5 shows a 5-s epoch of sway during an eyes open task and the cross-correlation functions derived during that epoch.

DISCUSSION

The main finding of this study was that there was little evidence of synchronization of soleus motor units bilaterally during standing. The extent of synchronization did not change when the eyes were open or closed, nor did it change when a voluntary isometric contraction was performed. On the other hand, pairs of motor units from within a single muscle showed

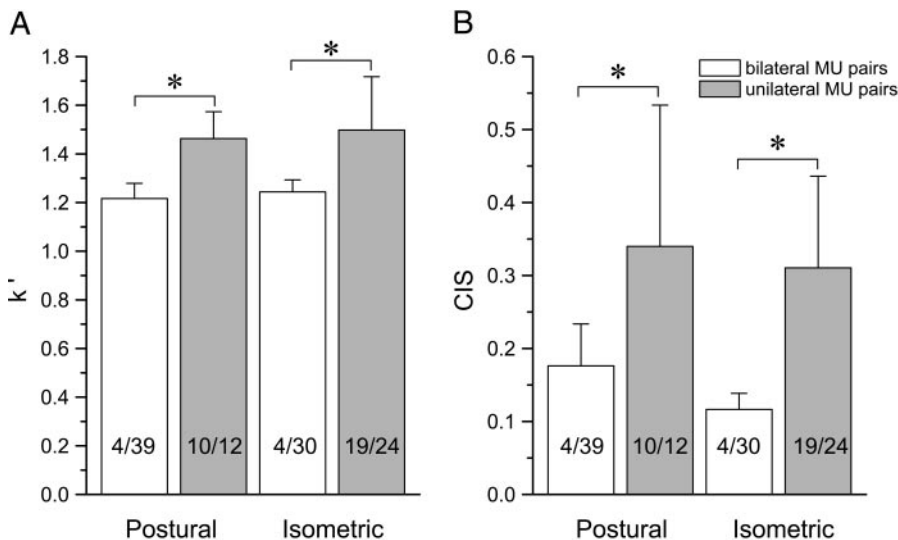


FIG. 3. Indices of synchronization, k' (A) and strength of common input (CIS) (B), during the eyes open postural task and voluntary isometric contractions. Mean \pm SD values for bilateral (open columns) and unilateral (gray columns) motor unit pairs that show significant synchronization are displayed. Both k' and CIS are significantly higher for the unilateral than the bilateral motor unit pairs (depicted with asterisks) in each task. Incidence of synchronization (significant/total pairs) is shown in each column.

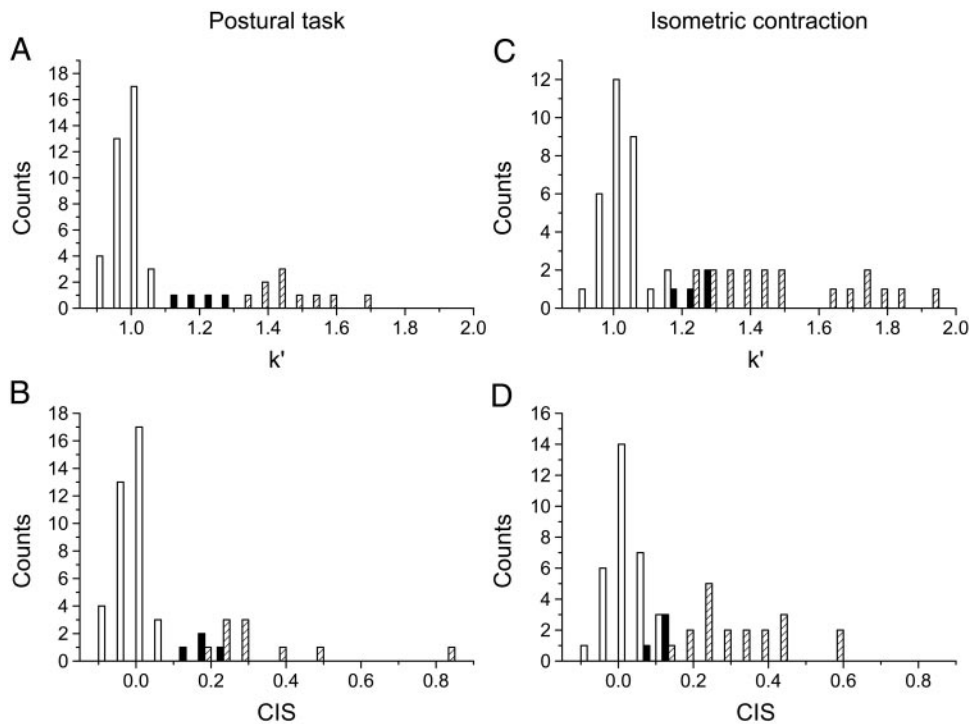


FIG. 4. Distributions of k' and CIS values during the eyes open postural task (A and B) and voluntary isometric contractions (C and D) for all motor unit pairs. Open bars, all nonsignificant pairs (bilateral and unilateral); filled bars, bilateral significant pairs; striped bars, unilateral significant pairs.

significantly more synchronization in both incidence and magnitude.

The low incidence of bilateral motor unit synchronization can be explained by taking the possible sources of synchronization into account. Short-term synchronization can be attributed to last order branching of presynaptic inputs (Sears and Stagg 1976). It has been observed in various hand muscles (Bremner et al. 1991; Garland and Miles 1997; Schmied et al. 1993) in which case the presynaptic input would likely be cortico-motoneuronal in origin (Farmer et al. 1993b). For the control of standing posture, the vestibulospinal tract, which makes monosynaptic connections to the ankle extensors in the cat (Grillner et al. 1970), would be a likely source for branched presynaptic inputs and short-term synchronization. In fact, Shinoda et al. (1986) showed that 5/15 axons originating in the lateral vestibulospinal tract of the cat had collaterals that extended to both the ipsilateral and bilateral ventral gray matter. However, the infrequent occurrences of these collaterals may indicate that bilateral vestibular projections cannot be solely relied on to provide the common presynaptic input to the soleus α -motoneuron pools between legs.

The absence of short-term synchronization in the soleus is not surprising considering the relative absence of direct corticospinal inputs to the soleus motoneuron pool (Brouwer and

Ashby 1990, 1992). In addition, studies involving both humans (Brouwer and Ashby 1990, 1992) and monkeys (Asanuma et al. 1979) have shown stronger corticospinal projections to the tibialis anterior compared with the soleus. Although short-term synchronization between bilateral soleus motor unit pairs was not found, broad peak synchronization was shown.

Broad-peak synchronization results from the synchronous firing of presynaptic inputs (Kirkwood et al. 1982). Spinal interneurons that branch extensively to multiple motoneurons (Jankowska and Lundberg 1981) may receive common descending inputs (Semmler 2002). Synchronous activity of the bilateral vestibulospinal pathways could produce motor unit synchrony in the postural musculature. The vestibulospinal tract originates in the lateral vestibular nucleus and descends unilaterally to the α -motoneuron pools innervating the triceps surae (Grillner et al. 1970). During quiet standing while keeping the head still, there may be minimal differences in afferent information from the vestibular apparatus to the vestibular nuclei between sides. Thus it could be assumed that the soleus α -motoneuron pools bilaterally would be receiving comparable inputs. However, given the evidence of lateral dominance in the vestibular system (Cernacek 1980) and in the cortical correlates of vestibular function (Dieterich et al. 2003; Fasold et al. 2002), it is possible that the input to the soleus musculature differs bilaterally. In fact, lateral hand dominance has been shown to affect the level of correlation between firing rates of concurrently active motor units (Kamen et al. 1992) and in the extent of synchronization (Semmler and Nordstrom 1995) between motor units of the first dorsal interosseous muscle. Thus the differences in the relative contributions from vestibular inputs may account for the low incidence of broad-peak bilateral synchronization.

In this study, the high correlation coefficients relating the COP excursions in the AP directions indicate that each leg was contributing almost equally to the amount of sway. The corre-

TABLE 1. Extent of sway in both the AP and ML directions for each leg and task

	AP Sway, mm		ML Sway, mm	
	Left	Right	Left	Right
Eyes open	6.16 \pm 2.15	6.80 \pm 2.45	0.96 \pm 0.72	1.10 \pm 0.81
Eyes closed	6.68 \pm 2.29	6.53 \pm 2.07	1.19 \pm 0.56	1.20 \pm 0.58

Values are mean \pm SD. There were no differences between tasks. AP, anteroposterior; ML, mediolateral.

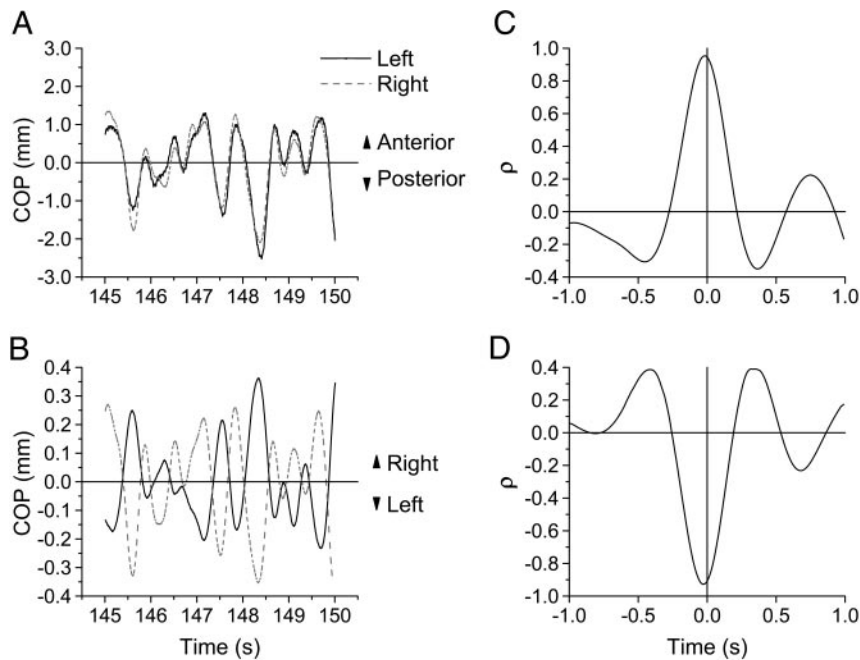


FIG. 5. Five-second epochs of sway in the anteroposterior (AP) (A) and mediolateral (ML) (B) directions for a single subject during the eyes open postural task. Note that AP sway is in phase, whereas ML sway is anti-phase. C and D: cross-correlation functions for the epochs in A and B, respectively, showing virtually no time lag between legs.

lations calculated in this study ($\rho = 0.80$ for eyes open and 0.83 for eyes closed) were very similar to those reported by Winter et al. (1993) with $\rho = 0.80$ and 0.86 for the eyes open and eyes closed tasks, respectively. It seems clear that both legs were sharing a common function. Despite this, the incidence of synchronized firing of bilateral motor units was low.

Synchronization of postural muscle motor units bilaterally may not be an efficient means of ensuring that the COP changes to match the changes in the position of the COM. Synchronization of motor units could result in a moment of force produced at the ankle exceeding that which is required based on the current position of the COM. However, independence in bilateral motor unit firing may ensure on-line sensitivity of the CNS to the changes in COM. Evidence from simulated muscle activity (Yao et al. 2000) indicates that synchronization of motor units increases the fluctuations in force. Because the COP is so tightly coupled to the ankle muscle activity and the resulting force that is produced (Gatev et al. 1999; Masani et al. 2003), the fluctuations in the forces that would be produced by synchronous motor units may have a deleterious effect on the ability of the CNS to produce muscle force that is appropriate for the position of the COM.

This study revealed both a higher incidence and magnitude of motor unit synchronization between unilateral motor unit pairs compared with bilateral pairs. This was the case for both the postural tasks and voluntary isometric contractions. Unilateral synchronization during a postural task may arise from projections from the lateral vestibular nucleus that are predominantly ipsilateral (Grillner et al. 1970; Mano et al. 1976). During a voluntary isometric contraction, corticospinal inputs would be expected to contribute substantially to the synaptic input to the soleus motoneuron pool. The relatively broad duration histogram peak (12.1 ms) observed in this study suggests presynaptic synchronization of descending inputs to the ipsilateral soleus α -motoneuron pool. The small amount of direct cortico-motoneuronal inputs to the lower limb (Brouwer and Ashby 1990) is consistent with the width of the histogram

peak. The data from the unilateral motor unit pairs during both postural task and voluntary isometric contraction were similar to that observed in previous studies. Nielsen and Kagamihara (1994) found significant synchronization in 89% (24/27) of soleus motor unit pairs, with an average peak width of 12.3 ms during an isometric contraction. The mean CIS values for the significant unilateral motor unit pairs in this study of 0.31 – 0.34 were within the range of values reported by Semmler and Nordstrom (1998) for first dorsal interosseous motor unit pairs in skill-trained and untrained individuals. Keen and Fuglevand (2004) reported similar values for pairs of motor units across compartments of the extensor digitorum muscle. However, whereas the mean significant CIS values of 0.31 – 0.34 were the highest observed in this study, similar values in previous studies (Keen and Fuglevand 2004; Semmler and Nordstrom 1998) were considered to be relatively low. Because synchronization was measured in the upper limb in the preceding studies, the contrast in the extent of synchronization is likely due to the differences in the extent of direct cortico-motoneuronal projections between the upper and lower limb (Brouwer and Ashby 1990) and the relatively small amplitude of EPSPs of both corticospinal and vestibulospinal origin propagating to hind limb motoneurons reported in studies with monkeys (Jankowska et al. 1975) and cats (Grillner et al. 1970).

The results of this study are in contrast to those reported by Gibbs et al. (1995), who showed that bilateral gastrocnemius multiunit spike trains were synchronized during a balancing task. In that study, 4/10 subjects showed bilateral synchronization during quiet standing. The incidence of bilateral synchronization increased to 7/10 subjects when the task difficulty increased (i.e., while balancing). The balancing task employed by Gibbs et al. (1995) involved standing on a board that pivoted in the sagittal plane. This type of challenge would constrain the perturbations of sway to one direction and may result in the increase in synchronized motor unit activity. In addition, this type of postural challenge would also require the subject to pay more attention to the task. Schmier et al. (2000)

have shown that synchronization increases with increases in the attentional demands in a task. On the other hand, the board-balancing task may have required subjects to control knee and/or hip position as well as ankle position. Because the contribution of the gastrocnemius to plantarflexor torque is dependent on both knee and ankle position (Herzog 2000; Kawakami et al. 1998), the changes in joint position that would more readily occur in this task compared with quiet stance may have led to the multi-unit synchronization observed in the gastrocnemius.

The eyes closed task employed in this study did not produce significant increases in the excursions of sway or the correlations of sway between legs. This may have resulted from the relatively wider base of support used by subjects when standing on separate force platforms. Subjects in studies involving a single platform have used a smaller base of support and have shown that both AP and ML sway increase when the eyes are closed (Dichgans et al. 1976; Lucy and Hayes 1985).

In summary, the incidence of bilateral soleus motor unit synchronization during standing postural tasks is sporadic, even when the conditions of the postural task become more difficult. However, motor unit pairs within a single soleus muscle are synchronized during the same postural tasks and are more strongly synchronized than the synchronous bilateral pairs. The incidence and extent of synchronization was similar between postural tasks and voluntary isometric contractions. While some level of motor unit synchronization is present during upright posture, a high level of synchronization is not a prerequisite for successful postural control.

GRANTS

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