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Is spinal excitability of the triceps surae mainly affected by muscle activity or body position?

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Cattagni T, Martin A, Scaglioni G. Is spinal excitability of the triceps surae mainly affected by muscle activity or body position? *J Neurophysiol* 111: 2525–2532, 2014. First published March 19, 2014; doi:10.1152/jn.00455.2013.—The aim of this study was to determine how muscle activity and body orientation contribute to the triceps surae spinal transmission modulation, when moving from a sitting to a standing position. Maximal Hoffmann-reflex (H_{\max}) and motor potential (M_{\max}) were evoked in the soleus (SOL), medial and lateral gastrocnemius in 10 male subjects and in three conditions, passive sitting, active sitting and upright standing, with the same SOL activity in active sitting and upright standing. Moreover volitional wave (V) was evoked in the two active conditions (i.e., active sitting and upright standing). The results showed that SOL H_{\max}/M_{\max} was lower in active sitting than in passive sitting, while for the gastrocnemii it was not significantly altered. For the three plantar flexors, H_{\max}/M_{\max} was lower in upright standing than in active sitting, whereas V/M_{\max} was not modulated. SOL H-reflex is therefore affected by the increase in muscle activity and change in body orientation, while, in the gastrocnemii, it was only affected by a change in posture. In conclusion, passing from a sitting to a standing position affects the H_{\max}/M_{\max} of the whole triceps surae, but the mechanisms responsible for this change differ among the synergist muscles. The V/M_{\max} does not change when upright stance is assumed. This means that the increased inhibitory activity in orthostatic position is compensated by an increased excitatory inflow to the α -motoneurons of central and/or peripheral origin.

H-reflex; V-wave; posture; triceps surae

THE MONOSYNAPTIC HOFFMANN REFLEX (H-reflex) has been extensively used to investigate the transmission efficiency of group Ia projection onto the α -motoneuron pool. It has been employed since the 1980s as an effective tool to investigate changes occurring at the level of the spinal loop in various functional motor performances, such as postural control (Capaday and Stein 1986; Trimble et al. 2000). It has been widely demonstrated that change in posture modulates the segmental reflex response which decreases as the complexity of the postural task increases. Several investigations have indeed shown that the H-reflex in the plantar flexors (PFs) is down-regulated when subjects are in a quiet standing condition compared with sitting (Katz et al. 1988; Kawashima et al. 2003) or to supine (Chalmers and Knutzen 2002) and prone positions (Angulo-Kinzler et al. 1998; Bove et al. 2006; Kocejka et al. 1993, 1995). This modulation could be the consequence of a change in body position and/or a change in the background

activity of the muscles involved in the postural task. Some of these authors, however, did not take into account the effect of the postural background electromyographic (EMG) activity, while others removed it, whether by comparing different passive conditions (i.e., supported and standing, limiting EMG activity as much as possible; Kawashima et al. 2003; Shimba et al. 2010), or by comparing equally active postural conditions (i.e., supported and standing, maintaining EMG activity constant in each stance; Bove et al. 2006). In this way, they bypassed the influence of the spontaneous activity of postural muscles on the transmission efficiency of Ia afferent α -motoneuron synapses, during an upright standing (US) task.

It has been extensively demonstrated that the H-reflex is modulated by voluntary muscle contraction. Facilitation was observed during an active sitting or prone condition compared with an equivalent passive condition. In this regard, a progressive increase in the soleus (SOL) H-reflex was observed at weak contraction intensities, ranging from 10 to 30% of the PFs maximum voluntary contraction (MVC) (Angulo-Kinzler et al. 1998; Stein et al. 2007).

A recent study has shown that, in US, the EMG activity of the calf muscles is around 10% of that recorded during their MVC (Billot et al. 2010). It is therefore interesting to note that, although the spontaneous contraction of postural muscles in the standing position is in the range of efforts facilitating the excitability of motoneurons, the H-reflex is generally down-regulated. Several neurological mechanisms, acting by means of presynaptic and/or postsynaptic inhibition of motoneurons, have been suggested in the literature as mediating H-reflex changes during different environmental conditions. However, before precise neurological mechanisms can be identified, a simple question needs to be addressed. If the H-reflex is potentiated by weak muscle activity but depressed by body position, what is the specific contribution of each of these factors to the transmission efficiency of the Ia afferent input, when standing posture is assumed? To address this question, we recorded the H-reflex on the SOL, medial gastrocnemius (MG) and lateral gastrocnemius (LG) in different experimental conditions: seated at rest, US and seated with a muscle activity equivalent to that produced during US. To compare H-reflex among subjects and conditions, its amplitude has to be normalized to the maximal compound action potential (M-wave) obtained in each condition (Zehr 2002). In active conditions, the maximal M-wave was evoked concurrently with an electrophysiological variant of the H-reflex called volitional wave (V-wave) (Aagaard et al. 2002; Pensini and Martin 2004; Upton et al. 1971). Although this measure is not yet perfectly understood, its amplitude has been reported to depend on

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motoneuron responsiveness and the synaptic transmission efficiency between Ia afferents and α -motoneurons (Pensini and Martin 2004; Racinais et al. 2013). It also reflects the magnitude of the descending corticospinal drive addressed to α -motoneurons (Aagaard et al. 2002; Duclay and Martin 2005; El Bouse et al. 2013; Pensini and Martin 2004; Upton et al. 1971). Because V-wave is a spinal reflex that partly involves the same neural circuitry as the H-reflex (Upton et al. 1971), recording both responses can provide information regarding the potential mechanisms (spinal and/or supraspinal) mediating neural adjustments during different experimental conditions.

Furthermore, we extended our investigation to the gastrocnemii, to complete observations of earlier studies which generally focused only on SOL H-reflex modulation with change in posture. Postural control requires the activation of the whole triceps surae group, which is composed of very different muscles as seen from the architectural, the myotopy (Johnson et al. 1973) or the innervation (Young et al. 1983) point of view. In this context, it seems reasonable to suppose that neural control may be muscle specific. Earlier studies support this assumption, showing that the modulation of the H-reflex amplitude may differ between SOL and MG according to the muscle contraction type (Duclay et al. 2008) and during different hopping tasks (Moritani et al. 1990). Moreover, if we consider 1) that the density of muscle spindles is more than two times higher in SOL than in gastrocnemii (i.e., SOL receives greater spindle feedback) (Tucker and Turker 2004; Voss 1971); 2) that the primary afferents principally depolarize slow-twitch α -motoneurons (Koerber and Mendell 1991; Lev-Tov 1987), the proportion of which is higher in SOL than in gastrocnemii, and finally 3) that presynaptic inhibition could be differently organized in gastrocnemii than in SOL (Nielsen and Kagamihara 1993), it can be expected that SOL and gastrocnemii H-reflexes are differently modulated by changes in posture and muscle activity.

In light of these considerations, the present study was thus designed to investigate how muscle activity and body orientation contribute to spinal transmission modulation in the triceps surae when moving from a sitting to a standing position. Comparison of the evoked H-reflex and V-wave should provide valuable insights into the potential mechanisms (spinal vs. supraspinal) mediating neural adjustment during US.

MATERIALS AND METHODS

Subjects

Experiments were performed on 10 healthy men (age 24.4 ± 2.3 yr, height 179.0 ± 5.2 cm, mass 70.4 ± 7.1 kg, means \pm SD) with no history of neurological and/or musculoskeletal disorders. All of the selected individuals were normally active, all were volunteers and all gave their written consent prior to participation in the investigation. Subjects had not engaged in any strenuous locomotor activity for at least 24 h before the experimental sessions. The protocol of the current investigation was approved by the University of Burgundy Committee on Human Research and was in conformity with the Declaration of Helsinki.

Experimental Setup

All measurements were carried out simultaneously on both lower limbs.

Mechanical recordings. Participants were examined in the seated position with the trunk inclined at 60° with reference to the vertical, knee joint angle at 160° and ankle joint angle at 90° . Feet were individually secured by two straps to the footplate of a dynamometer (Biodex, Shirley, NY). This securing of the feet may create a greater cutaneous sensory feedback in sitting conditions than in upright stance, which could induce a slight modulation of the reflex response (Pierrot-Desseilligny and Burke 2005) and thus alter the basis of comparison. A control experiment was carried out on five subjects to verify the effect of this securing of the feet on the evoked responses. We observed that M-wave, H-reflex, ratio of maximal H-reflex (H_{\max}) to maximal motor potential (M_{\max}) (H_{\max}/M_{\max}), and the submaximal M-wave evoked at H_{\max} ($M_{\text{at-}H_{\max}}$) were not modulated by strapping the feet. We can thus assume that our results were not affected by this methodological detail.

The center of rotation of the dynamometer shaft was aligned with the anatomical ankle flexion-extension axis. Subjects were securely stabilized by two crossover shoulder harnesses and a belt across the abdomen. Particular care was taken in monitoring subjects' posture and in avoiding head rotations during the test to maintain constant corticovestibular influences on the excitability of the motor pool and to limit afferent feedback from other peripheral receptors, i.e., Golgi tendon organs, cutaneous and joint afferences (Schieppati 1987; Zehr 2002).

Electromyographic recording. The subjects' skin was first carefully prepared by shaving, abrading and cleaning with alcohol, to obtain a low impedance (<5 k Ω). Then bipolar surface electrodes of 8-mm diameter with an interelectrode distance (center-to-center) of 2 cm were placed along the middorsal line of the leg, ~ 5 cm below the insertion of the two heads of the gastrocnemii on the Achilles tendon, for SOL measurements. MG and LG recording electrodes were fixed lengthwise over the middle of the muscle belly. Because the electrophysiological responses induced by tibial nerve stimulation are generated by the PFs and possibly contaminated by concomitant activation of the tibialis anterior (TA), the EMG activity of the antagonist muscle was also recorded. For this muscle, the electrodes were positioned at 1/3 on the line between the fibula and the tip of the medial malleolus (Duclay et al. 2009; Hermens et al. 2000). The reference electrode was placed in a central position between the two gastrocnemii bellies. The placement of the electrodes was marked on the skin with an indelible pen to ensure that the same recording site was used in the successive session. The EMG signal was amplified with a bandwidth frequency ranging from 10 Hz to 5 kHz (gain = 1,000). The EMG and mechanical signals were sampled at 2 kHz with the Biopac acquisition system and stored with commercially available software (Acqknowledge, MP 150) for off-line analysis.

Electrical stimulation. Electrophysiological responses, H-reflex, M-wave and V-wave were evoked by percutaneous stimulation of the posterior tibial nerve in the popliteal fossa with a single rectangular pulse (1 ms) automatically delivered by two synchronized Digitimer stimulators (model DS7, Hertfordshire, UK). The self-adhesive cathode (8-mm diameter, Ag-AgCl) was placed in the popliteal fossa, and the anode (5×10 cm, Medicompex, Ecublens, Switzerland) on the anterior surface of the knee. The electrical stimulation was optimized for the SOL muscle. For each leg, the optimum cathode position, namely the site where the greatest H-reflex potential in SOL was evoked, was located with a hand-held cathode ball (0.5-cm diameter). Once determined, the cathode electrode was firmly fixed to this site by taping. Since the electrical stimulation was optimized for the SOL, it is possible that gastrocnemii H-reflexes were submaximal at SOL H_{\max} intensity; instead they were found to be maximal or obtained in the ascending part of the recruitment curve for all subjects, as previously observed by Duclay et al. (2008) and Gondin et al. (2006). It should also be noted, as detailed in the subsequent section, that the H-M recruitment curves were plotted for each muscle to identify the maximal evoked responses (H-reflex, M-wave and V-wave) for each of them.

Experimental Protocol

Each subject was tested in three different experimental conditions: seated passively (SP), seated actively (SA) and US, carried out over two testing sessions (i.e., seated and standing), randomly administered. The two sessions lasted 2 h each and were interspaced by an interval of 1 day.

In the SA condition, differently from previous reports that confine their analysis to a single limb, the target muscle activity was obtained through the simultaneous contraction of both legs. This choice was made to better approximate the bipedal upright stance.

In each experimental condition, recordings started by progressively increasing the electrical stimulation intensity by 2 mA from the H-reflex threshold until the maximal M-wave. Four stimuli were delivered at each intensity, interspaced by a 10-s interval to avoid the confounding effect of homosynaptic postactivation depression (Hultborn et al. 1996). The average of the EMG signals obtained at the various intensities was used to plot the H-M recruitment curve for the SOL, MG and LG. These curves were analyzed off-line to identify, for each leg and PF muscle (SOL, MG, LG), the amplitude of H_{max} , M_{max} , $M_{at-Hmax}$ and the V-wave during muscle contraction (Fig. 1).

The first session started with a 40-s recording of the SOL EMG in the US posture. This initial recording allowed us to quantify the SOL EMG root mean square (RMS) (integration time: 0.5 s) needed to maintain the upright stance. This target activity was reproduced in the SA condition during which subjects were guided by visual EMG-RMS biofeedback on a computer screen placed at a distance of 1 m in front of them. More precisely, subjects performed four submaximal bilateral contractions corresponding to the target activity, each lasting 4 s and separated by a 6-s rest period. Electrical stimulations were applied 2 s after the beginning of the contraction, when the voluntary torque matched the target activity.

During the standing session, subjects maintained a comfortable posture. They held their arms freely at their sides, feet approximately shoulder width apart and in complete contact with the floor. Subjects were asked to remain as still as possible, looking straight ahead at a point located at eye height about 3 m away.

At the end of each session, two MVCs of the PFs and dorsiflexors (DFs), each separated by a 2-min rest period, were performed in the seated position. Throughout subjects' attempts to produce maximal effort, real-time visual feedback of the torque was displayed on a computer screen (Gandevia 2001), and stan-

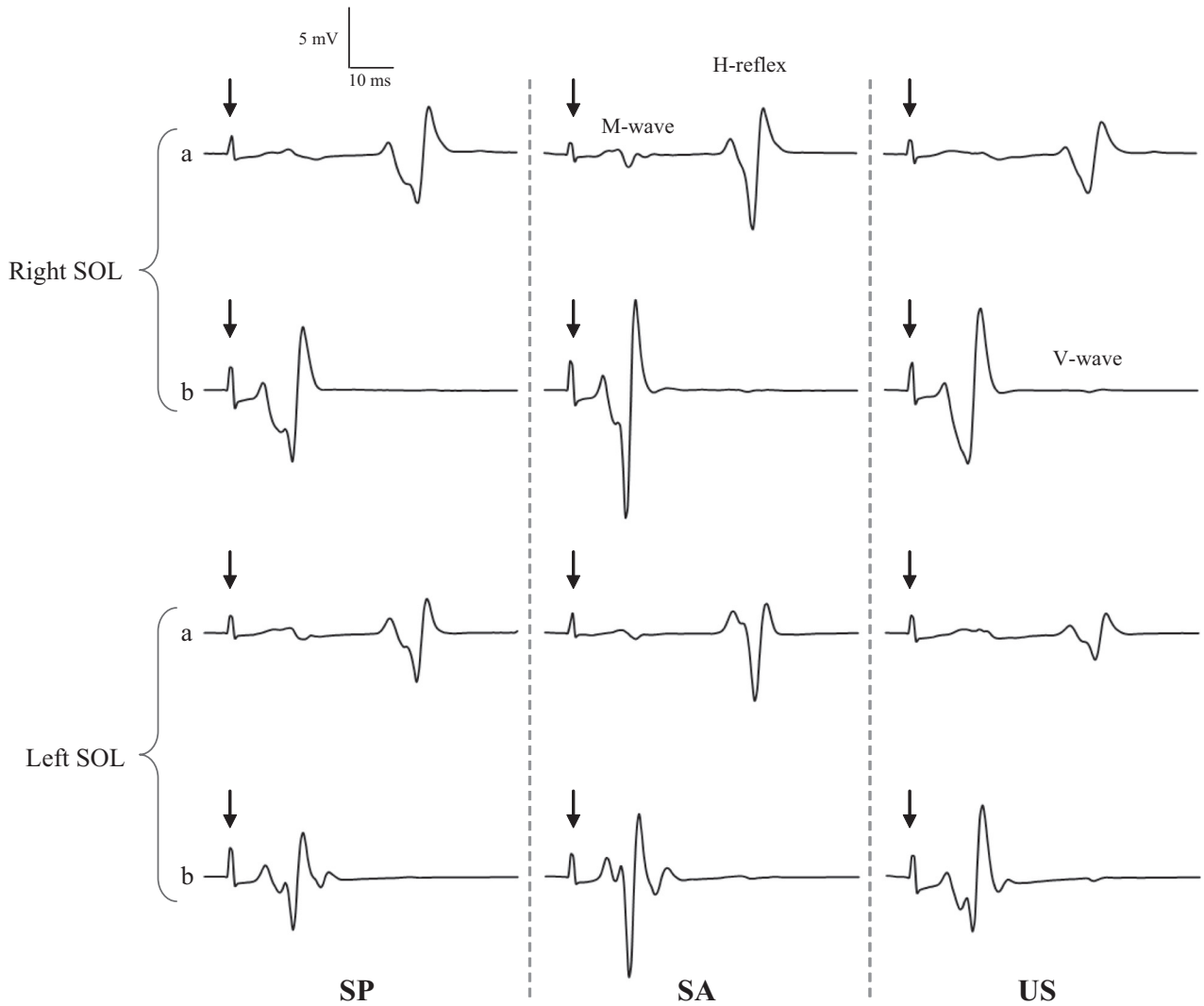


Fig. 1. Soleus (SOL) myoelectric responses in one representative subject. Typical recording of raw electromyographic (EMG) traces of the right (*top trace*) and left leg (*bottom trace*) is shown. *Trace a* corresponds to the recording obtained at maximal Hoffmann (H)-reflex (H_{max}) stimulation intensity, and *trace b* corresponds to the recording obtained at maximal motor potential (M_{max}) stimulation intensity in the three experimental conditions: seated passively (SP), seated actively (SA), upright standing (US). Muscle activity in SA corresponds to the EMG recorded during US for the SOL muscle. Arrows indicate the stimulus artifact. V-wave, volitional wave; M-wave, maximal compound action potential.

standardized verbal encouragements were also proffered during execution.

Data Analysis

Muscle strength. The PFs and DFs MVCs were determined as the highest torque value, measured over three trials.

The target PFs torque produced in the SA condition was analyzed over a 500-ms period preceding the electrical stimulation and calculated as being the mean over eight contractions. The average value was normalized to the PFs MVC torque.

Evoked potentials. For each muscle of the PFs group, the peak-to-peak amplitude of H_{max} , $M_{at-Hmax}$ and M_{max} and the V-wave were calculated as a mean over four recordings in each experimental condition. The H_{max}/M_{max} was calculated to assess the proportion of motor units activated by the Ia afferents and the V-wave-to-maximal M-wave ratio (V/M_{max}) to appraise the amount of the descending command (Pensini and Martin 2004). As potentials may be potentiated by muscle contraction, the peak-to-peak amplitude of M_{max} used for normalization was determined in each specific experimental condition. To ensure that the same proportion of α -motoneurons was activated by the electrical stimulation in each experimental condition, the $M_{at-Hmax}$ -to- M_{max} ratio ($M_{at-Hmax}/M_{max}$) obtained in the passive condition was compared with that obtained in the active condition (Grospretre and Martin 2012).

EMG activity. The EMG of the SOL, MG, LG and the TA muscles was recorded over a 500-ms period preceding each stimulation. For each PF muscle, the EMG-RMS was calculated as being the mean over eight recordings and then normalized to the respective M_{max} (RMS/M_{max}). The RMS of the TA was normalized to the maximal RMS obtained for the highest MVC over three recordings (RMS/RMS_{max}) (Hagood et al. 1990).

Statistical analysis. Normality criteria were tested using the Kolmogorov-Smirnov test. Three-factor ANOVAs with repeated measures [experimental condition (SP, SA, US) \times leg (right and left) \times muscle (SOL, MG, LG)] were performed on the H_{max} , M_{max} , H_{max}/M_{max} , $M_{at-Hmax}/M_{max}$. Three-factor ANOVAs with repeated measures [experimental condition (SA, US) \times leg (right and left) \times muscle (SOL, MG, LG)] were performed on V-wave and V/M_{max} . Three-factor ANOVAs with repeated measures [experimental condition (SA, US) \times leg (right and left) \times muscle (MG, LG)] were performed on gastrocnemii RMS/M_{max} . Two-factor ANOVAs with repeated measures [experimental condition (SA, US) \times leg (right and left)] were performed on SOL RMS/M_{max} and TA RMS/RMS_{max} . A two-factor ANOVA with repeated measures [session (1 and 2) \times leg (right and left)] was performed on TA RMS_{max} . A one-way ANOVA was performed on PFs and DFs MVC to determine the difference between sessions. When a main effect or a significant interaction was found, a post hoc analysis was made using Tukey's test. The critical level for statistical significance was set at 5%. All data are presented as means \pm SD. EMG ratios are presented as a percentage of M_{max} . Statistical analysis was performed using Statistica 10 (Statsoft, Tulsa, OK, USA).

RESULTS

The statistical analysis did not reveal any significant asymmetries between the two legs for either mechanical or neurophysiological responses in any of the three experimental conditions. Lateral dominance did not seem to affect spinal excitability, confirming previous observations by Alrowayeh and Sabbahi (2011).

Torque and EMG-RMS

The average PFs MVCs, measured at the beginning of each session, were equivalent (244.2 ± 17.5 N·m sitting session vs.

245.6 ± 16.6 N·m standing session), as were the DFs MVCs (92.3 ± 4.2 N·m sitting session vs. 93.5 ± 3.9 N·m standing session). The target torque developed in the sitting position, when subjects reproduced the SOL EMG-RMS activity recorded in US, was 28.2 ± 10.5 N·m, (i.e., $11.9 \pm 4.7\%$ of the PFs MVC). Because in SA subjects were asked to reproduce a SOL EMG activity similar to that recorded in US, the statistical analysis of RMS/M_{max} was performed separately for SOL and gastrocnemii.

The SOL RMS/M_{max} and TA RMS/RMS_{max} were similar in SA and US. The statistical analysis revealed a significant effect of muscle and experimental condition on gastrocnemii RMS/M_{max} without interaction. The RMS/M_{max} of gastrocnemii was significantly ($P < 0.05$) higher in SA compared with US and was higher in MG compared with LG (Table 1.).

Evoked Potentials

The amplitude of H_{max} was significantly higher ($P < 0.001$) for SOL than for MG and LG over the three experimental conditions (Table 2). Irrespective of muscle, no difference was observed in H_{max} between SP and SA. The SOL H_{max} was significantly ($P < 0.01$) higher in both sitting conditions compared with US ($+3.8 \pm 3.0$ mV for SP, and $+4.8 \pm 3.5$ mV for SA), while for gastrocnemii, no difference was observed among experimental conditions.

There was a significant effect of experimental condition and muscle without interaction on the M_{max} . The post hoc analysis showed that M_{max} was significantly ($P < 0.01$) lower in SP (-2.6 ± 1.5 mV) and US (-2.0 ± 2.3 mV) than in SA, and significantly ($P < 0.001$) lower in MG (-7.0 ± 3.8 mV) and LG (-8.6 ± 4.1 mV) than in SOL. No significant difference was observed between MG and LG.

There was a significant effect of muscle on the V-wave. The post hoc analysis showed that V-wave amplitude was lower in MG (-0.17 ± 0.19 mV) and LG (-0.26 ± 0.20 mV) than in SOL.

EMG Ratios

The ANOVA analysis revealed a significant interaction between experimental condition (SP, SA, US) and muscle (SOL, MG, LG) on H_{max}/M_{max} . The SOL H_{max}/M_{max} was downmodulated by muscle activity; in fact, it was significantly ($P < 0.05$) lower in SA than in SP ($-9.8 \pm 9.4\%$). The SOL ratio was also downmodulated by body position, thus lower in US than in SA ($-13.3 \pm 11.6\%$; $P < 0.05$) (Fig. 2).

Table 1. Effect of experimental conditions (i.e., seated actively and upright standing) on RMS/M_{max} of soleus, medial gastrocnemius, lateral gastrocnemius, and RMS/RMS_{max} of tibialis anterior

	Muscle	SA	US
$(RMS/M_{max}) \cdot 10^2$	SOL	0.21 ± 0.09	0.22 ± 0.10
	MG	0.49 ± 0.40	0.29 ± 0.16
	LG	0.24 ± 0.14	0.12 ± 0.03
$RMS/RMS_{max}, \%$	TA	1.24 ± 0.57	1.31 ± 1.63

Values are means \pm SD, $n = 10$ subjects. RMS/M_{max} , root mean square (RMS) normalized to maximal motor potential (M_{max}); RMS/RMS_{max} , RMS normalized to maximal RMS; SOL, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; TA, tibialis anterior; SA, seated actively; US, upright standing.

Table 2. Effect of experimental conditions (seated passively, seated actively, upright standing) on amplitude of evoked potentials, for soleus, medial gastrocnemius, and lateral gastrocnemius

Muscle	SP	SA	US
SOL, mV			
H _{max}	10.57 ± 4.63	11.55 ± 5.64	6.75 ± 2.96
M _{max}	15.56 ± 5.13	19.53 ± 5.84	15.42 ± 4.71
V		0.26 ± 0.17	0.32 ± 0.22
MG, mV			
H _{max}	2.14 ± 0.90	2.82 ± 1.21	1.74 ± 0.98
M _{max}	8.50 ± 3.53	10.96 ± 4.26	9.97 ± 3.38
V		0.15 ± 0.06	0.11 ± 0.05
LG, mV			
H _{max}	2.10 ± 0.62	2.26 ± 0.74	1.35 ± 0.55
M _{max}	7.62 ± 3.39	9.00 ± 3.31	8.22 ± 2.38
V		0.04 ± 0.04	0.03 ± 0.03

Values are means ± SD, $n = 10$ subjects. H_{max}, maximal Hoffmann-reflex; V, volitional wave; SP, seated passively.

In the gastrocnemii, the H_{max}/M_{max} was significantly ($P < 0.05$) lower in US than in SP (MG: $-10.2 \pm 10.4\%$; LG: $-14.5 \pm 14.7\%$) and SA (MG: $-9.5 \pm 10.1\%$; LG: $-10.7 \pm 9.7\%$).

The M_{at-Hmax}/M_{max} was similar in the three experimental conditions but was higher in MG ($+28.2 \pm 30.9\%$) and LG ($+23.8 \pm 31.6\%$) than in SOL.

The statistical analysis of V/M_{max} revealed no experimental condition effect, but a significant muscle effect. V/M_{max} was significantly ($P < 0.01$) higher in SOL ($+1.0 \pm 0.9\%$) and MG ($+1.0 \pm 1.0\%$) than in LG.

DISCUSSION

The aim of the present study was to investigate the contribution of muscle activity and body orientation on the spinal transmission modulation of PFs, observed when upright posture is assumed. The primary finding of this study is that, although the three sections of the triceps surae exhibit similar behavior in terms of spinal excitability, the neural mechanisms responsible for this modulation differ among the three synergist muscles when the postural task becomes more complex. The SOL H_{max}/M_{max} is downmodulated by the increase in muscle background activity and change in body position, while for both gastrocnemii, H_{max}/M_{max} appears to be exclusively modulated by body position.

Methodological Considerations

It has been widely demonstrated in the literature that certain methodological requirements must be respected to ensure accurate analysis of the H-reflex in different experimental situations because results can be influenced by recording conditions (Chen and Zhou 2011; Zehr 2002). A number of factors may be used to help check the stability of recording conditions, including the constancy of the M-wave evoked concurrently with the H-reflex (Schieppati 1987). In the present investigation, the SOL M_{at-Hmax} represented $\sim 10\%$ of the SOL M_{max} in all the experimental conditions, in agreement with earlier values reported in the literature (Grospretre and Martin 2012; Maffiuletti et al. 2001; Scaglioni et al. 2003). Despite the fact that M_{at-Hmax} was more variable in gastrocnemii and represented

$\sim 30\%$ of the M_{max}, again no statistical difference was observed among experimental conditions. It can thus be assumed that the same proportion of α -motoneurons was activated by the electrical pulse in each condition. Yet background EMG activity, which could also induce changes in H-reflex amplitude (Schieppati 1987), did not differ between the two active conditions (i.e., SA and US) in SOL, but was higher in SA than in US in both gastrocnemii. This is due to the fact that SOL was the muscle of reference; indeed, in SA, subjects were asked to perform a muscle contraction corresponding to the level of SOL EMG-RMS activity recorded in US.

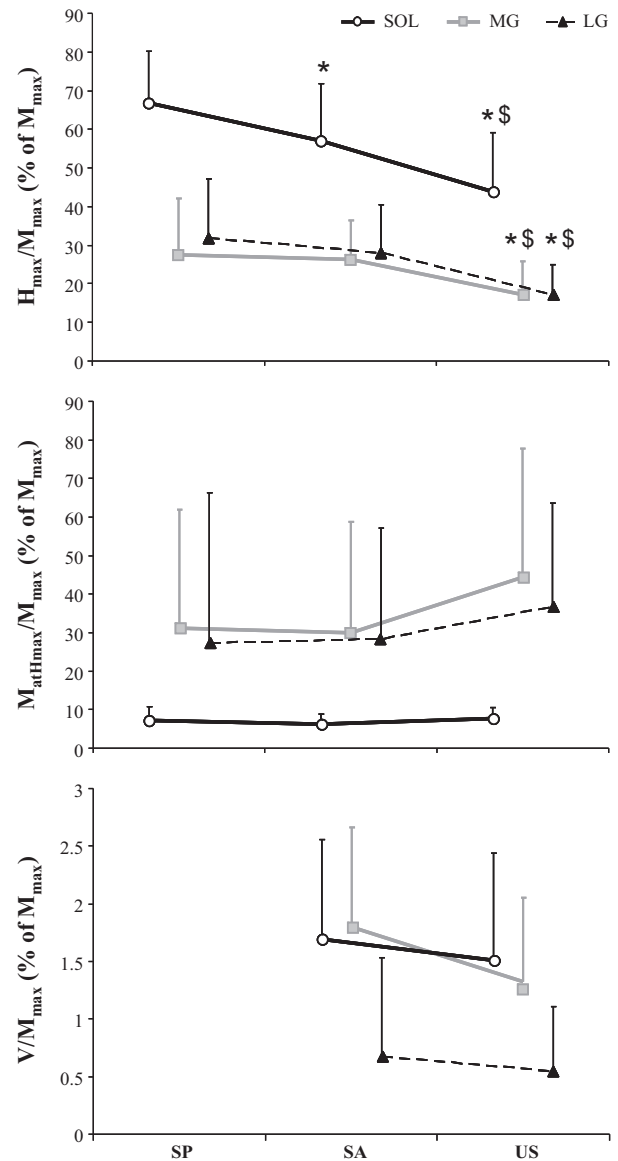


Fig. 2. Mean data of H_{max}-to-M_{max} ratio (H_{max}/M_{max}), submaximal M-wave evoked at H_{max}-to-M_{max} ratio (M_{at-Hmax}/M_{max}), and V-wave-to-M_{max} ratio (V/M_{max}) recorded on the SOL, medial gastrocnemius (MG), and lateral gastrocnemius (LG). H_{max}/M_{max} (A), M_{at-Hmax}/M_{max} (B), and V/M_{max} (C) are expressed as percentages of M_{max}. These ratios were calculated for the SOL (white symbols), MG (gray symbols), and LG (black symbols) and for the three experimental conditions: SP, SA, US. The M_{max} used for normalization was evoked in each specific condition and for each muscle. Values are means ± SD; $n = 10$ subjects. *Significant difference from SP, $P < 0.05$. §Significant difference from SA, $P < 0.05$.

In the sitting session, the knee joint was slightly flexed compared with the upright stance (160° vs. $\sim 180^\circ$) to avoid maintaining joint hyperextension for the entire duration of the session (~ 2 h).

Our results showed that M_{\max} was potentiated by voluntary contraction. We thus used the M-wave evoked in each specific experimental condition for the normalization of evoked potentials, as suggested in earlier investigations (Pensini and Martin 2004; Ruegg et al. 1990; Zehr 2002).

Effect of EMG Activity on the Reflex Loop Output

The present investigation shows that, for muscle contractions of around 10% of the MVC, the SOL EMG activity downmodulates the reflex response compared with rest (H_{\max}/M_{\max} : -10%), while earlier studies found an increase in SOL H-reflex amplitude for similar contraction intensities. To understand the reason for the discrepancy between present and previous findings, it is worth mentioning that, in most of these reports, the reflex response was not normalized by the M_{\max} obtained in the same experimental condition (Angulo-Kinzler et al. 1998; Hultborn and Pierrot-Deseilligny 1979), and in one of them it was not normalized at all (Angulo-Kinzler et al. 1998). It should be noted, simply for the sake of clarity, that, in the present study, the SOL H_{\max} was not modulated by the weak contraction, but M_{\max} increased, suggesting a facilitation of the neuromuscular transmission and/or a possibly enhanced electrogenic Na^+/K^+ pumping (Fitch and McComas 1985).

However, our divergent result could, at least in part, stem from the fact that, unlike previous investigations, we asked our subjects to perform bilateral, instead of unilateral, contractions (Angulo-Kinzler et al. 1998; Butler et al. 1993; Hultborn and Pierrot-Deseilligny 1979; Stein et al. 2007). This was done to be as close as possible to the neuromuscular conditions of bipedal stance. As a matter of fact, previous investigations showed that torque produced during maximal bilateral contractions is less than the sum of two maximal unilateral contractions (Howard and Enoka 1991; Kawakami et al. 1998; Matkowsky et al. 2011). Yet, during unilateral contractions, the functional MRI cortical activation is greater than one-half of that observed during bilateral contractions (Post et al. 2007). Although the level of effort was not submaximal in these studies as it was in the present report, these results would tend to suggest that the activation strategy might differ in unilateral and bilateral contractions. More directly, it was observed that bilateral contractions have a different impact on the efficiency of spinal transmission than unilateral contractions. It has, in fact, been shown that, during unilateral muscle efforts (i.e., 25–100% MVC), the amplitude of H-reflex decreases in the contralateral limb (Hortobagyi et al. 2003; Kawakami et al. 1998).

Moreover, it is also tempting to speculate that motoneuron excitability may be differently modulated during very weak compared with stronger muscle contractions. The lower H_{\max}/M_{\max} ratio observed at 10% of the MVC compared with rest implies a different control of the reflex loop output in weak contractions. It could be hypothesized that supraspinal influences produce presynaptic inhibition by depolarization of the afferent axons to control the very low level of effort. Nevertheless, whether presynaptic inhibition is involved in decreasing force contraction is a question requiring further study, since

a simple reduction in voluntary drive would reduce motoneuron excitability. In any case, the most generally accepted explanation for the disfacilitation of the reflex response currently remains postsynaptic recurrent inhibition. Hultborn and Pierrot-Deseilligny (1979) indeed observed, even though during unilateral contractions, that the excitation of Renshaw cells by the descending input tends to be greater for contraction intensities of $\sim 10\%$ of the MVC than at rest or for stronger contractions.

Although MG and LG were synergists of SOL, their H_{\max}/M_{\max} were not modulated by muscle contraction as was the case for SOL. Possible explanations for this different behavior may be found in their different biomechanical configuration (i.e., monoarticular vs. biarticular muscles) and in their Ia afferent/motoneuron connection. It has been demonstrated that the relative facilitation/depression depends on the target motoneuron. Depression appears to be dominant in low-threshold slow motoneurons, while high-threshold fast motoneurons seem to be less sensitive to inhibition (Koerber and Mendell 1991; Lev-Tov 1987). Since SOL includes ~ 70 – 90% slow and 10 – 30% fast-twitch fibers, while MG and LG have both types of fibers in approximately equal proportions (Johnson et al. 1973), their different compositions could account, at least in part, for their different susceptibility to the inhibitory mechanisms. Furthermore, as suggested by Nielsen and Kagamihara (1993), presynaptic inhibition may be differently controlled in gastrocnemii and in SOL motoneuronal pools. Therefore, the lack of modulation of the gastrocnemii H-reflex amplitude by the muscle contraction could be due to the different biomechanical configuration of these synergists compared with SOL and to the fact that the gastrocnemii may be less affected by peripheral inhibitory mechanisms.

Effect of Body Position on the Reflex Loop Output

In agreement with previous findings on SOL, the present study bears out the report that US downregulates, compared with a supported position, the reflex response of the three sections of the triceps surae (Alrwayeh et al. 2011; Angulo-Kinzler et al. 1998; Bove et al. 2006; Chalmers and Knutzen 2002; Katz et al. 1988; Kawashima et al. 2003; Koceja et al. 1993, 1995; Mynark and Koceja 1997). The decrease in reflex excitability observed in the three synergist muscles might reflect an increased activity in the inhibitory pathways meant to reduce the stretch reflex sensibility of the muscles, and thus to avoid the occurrence of reflex-mediated joint oscillation during a postural task. More precisely, our analysis showed that the SOL H_{\max}/M_{\max} was 13% less in the standing compared with the sitting position with an equivalent background EMG activity. This finding is in accordance with data from previous studies such as that of Bove et al. (2006), who recorded an H_{\max}/M_{\max} which was 10% lower in standing compared with an active lying position. The similarity of our results suggests that the possible differences in activation strategy between unilateral and bilateral contraction do not affect the modulation of the H_{\max}/M_{\max} due to the change in posture. In addition, Kawashima et al. (2003) found a SOL H_{\max}/M_{\max} depression of $\sim 10\%$ in moving from sitting to standing, and Shimba et al. (2010) observed a depression of $\sim 11\%$ from supine to standing. It should, however, be mentioned that, in these two latter studies, a different methodology was applied whose objective

was to avoid muscle contraction; measurements were carried out while trying to reduce, as much as possible, the EMG activity of the SOL (passive US).

As previously mentioned, we also observed that the gastrocnemii have the same behavior as that of the SOL when passing from SA to US, with an H_{\max}/M_{\max} decrease of 9% for MG and 11% for LG. This observation confirms the results of an earlier study (Alrowayeh et al. 2011) in which, however, the comparison was made between a passive prone position and standing and, therefore, without taking into account the effect of the postural background EMG activity. In addition to confirming this anterior report, our study further demonstrates that, differently from SOL, the reflex excitability of gastrocnemii is solely dependent on body position. It thus appears that change in posture affects the H_{\max}/M_{\max} of the whole triceps surae, but that the neuromuscular mechanisms responsible for this down-regulation may differ among synergist muscles.

The V-wave is an electrophysiological variant of H-reflex elicited by supramaximal stimulation intensities superimposed during voluntary muscle contraction. It consists in a volley of reflex impulses that are allowed to reach the muscle because of the removal of antidromic impulses by collision with the efferent neural drive generated by the voluntary contraction (Hultborn and Pierrot-Deseilligny 1979; Upton et al. 1971). It, therefore, reflects changes in the level of efferent and descending corticospinal drive. In the present study, the V/M_{\max} of the three PFs was not modulated by assuming the upright posture. This result corroborates a previous finding by Soto et al. (2006) on motor-evoked potential, a measure of the cortico-spinal excitability that results, like the V-wave, from solicitation of the neural system as a whole. These authors did not observe any modulation of the motor-evoked potential, elicited on SOL by transcranial magnetic stimulation, between a sitting active and a standing condition. This means that, in the two conditions, the final drive addressed to the motoneurons is the same. However, differently from Soto et al. (2006), the H-reflex allows us to differentiate the spinal from supraspinal contribution. The steadiness of the V-wave associated with the down-regulation of the H-reflex, when the US position is taken, indicates a compensation of the spinal excitability by an increase of the supraspinal drive. More specifically, because PFs RMS/M_{\max} did not differ according to the experimental condition, the amount of antidromic collision was thus theoretically the same when the subject passed from sitting to standing, while, on the contrary, spinal excitability (H_{\max}/M_{\max}) decreased. This means that reflex inhibition, present during upright posture, was compensated by neural mechanisms that may influence V-wave amplitude. In other words, the excitatory inflow to the α -motoneurons was higher when the subject was upright to compensate for their reduced excitability. This could be accounted for by an enhanced neural drive in the descending corticospinal pathways, with the consequence of increasing cancellation of the antidromic impulses and allowing more of the evoked H-reflex volley to reach the muscle. However, the increased excitatory inflow to motoneurons may also rely on neural mechanisms at the spinal level, to which the V-wave may also be sensitive. It should, indeed, be noted that the supramaximal level of nerve stimulation used during recording of the V-wave causes massive excitation of all afferent axons in the peripheral nerve (i.e., Ia large and small and II muscle spindle afferents), whereas the H-reflex

primarily relies on the pool of smaller motoneurons (Aagaard et al. 2002). Differently from Soto et al. (2006), who conclude that postural contraction in US and voluntary contraction in SA involve the motor cortex in a similar way, our results go as far as to suggest a greater engagement of supraspinal centers in postural control.

In conclusion, this investigation shows that weak muscle contraction (i.e., $\sim 10\%$ of the MVC), differently from stronger muscle effort (i.e., more than 40% of the MVC), does not potentiate the SOL H-reflex response, but unexpectedly down-regulates it. This supposes a different control of the reflex loop output during very low compared with greater muscle efforts. When passing from sitting to standing, the activity of lower limb muscles increases, and body position is modified. Our results show that the SOL H-reflex is sensitive to both of these modifications, and that both similarly affect the segmental reflex response, accounting, respectively, for 10 and 13% of the downmodulation in α -motoneuron excitability. On the other hand, gastrocnemii were more sensitive to change in posture (H_{\max}/M_{\max} : $\sim 12\%$ lower in US compared with SA) than to muscle activity (H_{\max}/M_{\max} : $SP \approx SA$). To explain these differences between the SOL and its synergists, we evoked a muscle-specific susceptibility in spinal excitability to the inhibitory mechanisms. This means that, although passing from sitting to standing affects the H_{\max}/M_{\max} of the whole triceps surae, the neural mechanisms responsible for this change may differ among synergist muscles. It was also observed that PFs V/M_{\max} was not modulated by assuming the upright posture while the α -motoneuron excitability decreased. This means that the increased activity of the reflex inhibitory mechanisms in the upright posture is compensated by an increased excitatory inflow to the α -motoneurons of central and/or peripheral origin.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: T.C., A.M., and G.S. conception and design of research; T.C., A.M., and G.S. performed experiments; T.C. analyzed data; T.C., A.M., and G.S. interpreted results of experiments; T.C. prepared figures; T.C. and G.S. drafted manuscript; T.C., A.M., and G.S. edited and revised manuscript; T.C., A.M., and G.S. approved final version of manuscript.

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