Corticospinal excitability during walking in humans with absent and partial body weight support

Maria Knikou a,b,c,⇑, Nupur Hajela b, Chaithanya K. Mummidisetty b

a Graduate Center/Department of Physical Therapy, City University of New York, NY, USA
b Sensory Motor Performance Program, Rehabilitation Institute of Chicago, Chicago, IL, USA
c Department of Physical Medicine and Rehabilitation, Northwestern University Feinberg School of Medicine, Chicago, IL, USA

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Highlights
• MEPs are modulated in a phase-dependent pattern under conditions of reduced body loading.
• The phase-dependent modulation pattern of the MEPs recorded from ankle muscles is reproducible over time.
• Reduced body loading utilized for gait rehabilitation will not change the strength of corticospinal drive.

Abstract
Objective: To establish changes in corticospinal excitability with absent and partial body weight support (BWS), and determine test–retest reliability of motor evoked potentials (MEPs) recordings during stepping in healthy humans.

Methods: The tibialis anterior (TA) and soleus MEPs during stepping at 0 and at 25 BWS were recorded in two experimental sessions in the same subjects. Transcranial magnetic stimulation was delivered randomly across the step cycle at 1.2 TA MEP resting threshold. The non-stimulated associated electromyogram (EMG) was subtracted from the TA and soleus MEPs at identical time windows and bins of the step cycle, and the resultant values were normalized to the maximal homologous EMG activity during stepping. The relationship between MEPs and background EMG activity was determined for each BWS level and session tested.

Results: The TA MEPs were facilitated at heel contact, progressively decreased during the stance phase, and facilitated throughout the swing phase of the step cycle. In contrast, the soleus MEPs were progressively increased at early-stance, depressed at the stance-to-swing transition, and remained depressed throughout the swing phase. The TA and soleus MEPs were modulated in a similar pattern across sessions at 0 and at 25 BWS, and were linearly related to the associated background EMG activity.

Conclusions: These results provide evidence that reduced body weight loading does not alter the strength of corticospinal excitability, and that MEPs can be reliably recorded at different sessions during stepping in healthy humans.

Significance: A rehabilitation strategy to restore gait in neurological disorders utilizes BWS during stepping on a motorized treadmill. Based on our findings, the strength of corticospinal drive will not be affected negatively during stepping under conditions of partial body loading.

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1. Introduction

Spinal neuronal networks integrating sensory afferent feedback interact continuously with supraspinal centers to produce efferent activity appropriate to the task and to the phase of the step during walking (task- and phase-dependent neuronal activity) (Nielsen, 2003; Knikou, 2010, 2012). However, most of evidence on the role of motor cortex in the neural control of locomotion comes from experiments conducted in the cats (Armstrong and Drew, 1984; Drew et al., 2002). Consequently, studying how corticospinal drive...
adapts under different conditions of sensory feedback can provide valuable information on the supraspinal control of human locomotion.

The modulation patterns of the ankle stretch reflex, quadriceps tendon reflex, and electrically induced soleus or quadriceps H-reflexes during walking are well established in humans. These reflexes increase progressively during the stance phase, are depressed at the stance-to-swing transition phase, while at late-swing and at heel contact the reflex amplitude is increased compared to the other phases of the step cycle (Capaday and Stein, 1986; Crenna and Frigo, 1987; Dietz et al., 1990a,b; Edamura et al., 1991; Yang and Whelan, 1993; Sinkjaer et al., 1996; Andersen and Sinkjaer, 1999; Larsen et al., 2006; Knikou et al., 2009a). The amplitude of the transcranial magnetic stimulation (TMS) induced motor evoked potentials (MEPs), recorded from the tibialis anterior (TA) and gastrocnemius medialis muscles, is modulated in a phase-dependent pattern during human walking (Schubert et al., 1997). The TA MEP amplitude increases before swing phase initiation and at late-swing, while the gastrocnemius medialis MEP amplitude increases at mid and late-stance phases (Schubert et al., 1997). Although the phase-dependent amplitude modulation of MEPs did not follow linearly the gait-mediated modulation of electromyographic (EMG) activity (Schubert et al., 1997), they are generally facilitated when the muscle from which they are recorded is active and small when the antagonist muscle is active (Schubert et al., 1997; Capaday et al., 1999). These findings suggest that the TA and soleus MEPs are modulated in a reciprocal pattern, similar to that known for the spinal reflexes.

Proprioceptors that transmit information about the amount of body loading contribute to the spinal reflex-mediated regulation of locomotion (Dietz, 2002; Knikou, 2010). Thus, one would expect that under conditions of reduced body loading, the function of the spinal reflex circuits that are prone to descending control would be altered. We have recently shown that the soleus H-reflex, reciprocal inhibition, and presynaptic inhibition phase-dependent modulation pattern remains unaltered when body weight support (BWS) is provided during stepping or when stepping in a specific limb trajectory imposed by a robotic exoskeleton (Knikou et al., 2009a, 2011; Mummidisetty et al., 2013). Collectively, in this study we established the modulation pattern of the MEPS across multiple phases of the step cycle in healthy humans during stepping with absent and partial BWS. We also recorded MEPS in the same subjects under identical experimental procedures 2–7 days after the first experiment, in order to establish test–retest reliability of MEPS recordings during stepping.

2. Methods

2.1. Subjects

People with tooth implants, assistive hearing devices, pacemaker, history of seizures, and medications known to alter central nervous system excitability were excluded from participation. Seven healthy volunteers with an age range of 23–44 years (27.7 ± 7.4, mean ± SD) participated in the study. All subjects signed an informed consent form for neurophysiological tests before study participation, which was approved by the Northwestern University (IL, USA) institutional review board. The study was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Experimental procedures

The purpose of this study was to establish the modulation pattern of the MEPs recorded from the TA and soleus muscles, and demonstrate test–retest reliability of MEPS recordings with absent and partial BWS during treadmill walking. With the subjects seated, bipolar differential surface electrodes of fixed inter-electrode distance (Motion Lab Systems Inc., Baton Rouge, LA, USA) were placed on the right (contralateral to the magnetic coil) TA and soleus muscles following standard procedures for EMG recordings. Single 1-ms TMS pulses over the left primary motor cortex were delivered with a Magstim 200 stimulator (Magstim, UK) via a 110 mm double-cone coil and the induced current to flow in a posterior-to-anterior direction. The point where the lines between the inion and glabellum, and the left and right ear tragus met was marked on an EEG cap. The double-cone coil was placed parallel and approximately 1 cm posterior and 1 cm lateral to the left from this intersection point. With the double-cone coil held at this position, the stimulation intensity was gradually increased and the MEPS recorded from the right TA and soleus muscles were observed on a digital oscilloscope (TDS 2014, Tektronix, Beaverton, OR, USA). When in three out of five TMS pulses, MEPS could not be evoked at low stimulation intensities with the subject at rest in the TA muscle only, the magnetic coil was moved by few mm and the procedure was repeated. When the optimal position was found, the TA MEP resting threshold was established and corresponded to the stimulation intensity that induced repeatable MEPS in size that were approximately 100 μV of peak-to-peak amplitude (Rossini et al., 1994; Rothwell et al., 1999). Ten MEPS, each evoked once every 10 s, were recorded at 1.0 and at 1.2 times the MEP resting threshold. Then, the MEP input–output curve was constructed, and the optimal position of stimulation was marked again on an EEG cap for each subject.

Then, the subject stood on the treadmill, and wore an upper body harness that was connected through an overhead pulley to the frame of the TheraStride™ system (Innovovent, St. Louis, MO, USA) (Fig. 1A), and a mouth guard and ear plugs to minimize discomfort due to TMS. The magnetic coil was positioned on the head, and the optimal stimulation position was verified again with the subject standing, based on the procedures utilized during seated. The position of the magnetic coil was maintained through a customized chin strap and was supported by a Velcro connected to the frame of the TheraStride system (Fig. 1A). With the subject standing, the right leg was held by an experimenter in a flexed and/or in an extended position without being loaded, and the TA MEP resting threshold was re-established. Ten MEPS, each evoked once every 10 s, were recorded at 1.0 and at 1.2 times the MEP resting threshold with the leg extended or flexed. In the first experimental session, the mean TA MEP resting threshold with the right leg flexed and extended during standing on the left leg was 38.4 ± 6.1 (mean ± SD)% and 45 ± 6.6% of the stimulator output, respectively. In the second experimental session, the mean TA MEP resting threshold with the right leg flexed and extended during standing on the left leg was 38.4 ± 6.1% and 45.3 ± 6.6% of the stimulator output, respectively.

With the subject standing, the right common peroneal nerve was stimulated with a single shock of 1-ms duration, that was triggered from a computer (controlled by customized Labview software) and delivered by a constant current stimulator (DS7A, Digitimer, UK). The stimulus to the common peroneal nerve was delivered by a bipolar stainless-steel electrode placed distal to the head of the fibula. The stimulation intensity corresponding to the TA maximal M-wave was established, and 10 TA maximal M-waves, each evoked once every 5 s, were recorded.

The treadmill speed for all subjects was set at 0.98 m/s, which corresponds to a comfortable medium gait speed (Bohannon, 1997). The TMS output was adjusted at 1.2 times the TA MEP resting threshold while subjects stepped at 0 and at 25 BWS. TMS delivered at 1.2 MEP threshold corresponded largely to the linear portion of the TA MEP input–output curve constructed with the
subjects seated (Fig. 1B). The pulse delivered to the MagStim during stepping was triggered based on the signal from the right foot switch (Biopac Systems, TSD-111, CA, USA). In all subjects, TMS was delivered every three steps randomly across the step cycle which was divided into 16 equal time windows or bins. Bin 1 corresponds to heel contact. Bins 8, 9, and 16 correspond approximately to stance-to-swing transition, swing phase initiation, and swing-to-stance transition, respectively. For each subject, at least ten MEPs were recorded at each bin. The procedures in the second experimental session, which was conducted 2–7 days after the first session, were identical to those utilized in the first session. Reliability of EMG recordings is supported by the similar TA maximal M-waves recorded at both sessions (Fig. 1C). During the experimental sessions, EMG, foot switch, and amplitude of body unloading were recorded at 2000 Hz with custom written software (National Instruments, Austin, TX, USA).

2.3. Data analysis

Offline data analysis started with identification and marking of the right and left foot switches, and identification of MEPs with customized Labview scripts. EMG signals during stepping were band-pass filtered 40–500 Hz and rectified. The TA MEP size at each bin of the step cycle was measured as the linear EMG envelope starting at 25 ms post-TMS for 60-ms. The TA linear EMG envelope at each bin for steps without stimulation (control EMG) was determined at identical time delays and duration. The average control EMG was subtracted from the TA MEPs, and the resultant subtracted TA MEPs values were normalized to the maximal TA EMG activity during stepping. This subtraction resulted in negative values when the MEP was smaller from the control EMG and positive values when the MEP was larger from the control EMG (Knikou et al., 2009b). To establish the maximal EMG activity, EMG signals during stepping without TMS, were full-wave rectified, high-pass filtered at 20 Hz, and low-pass filtered at 500 Hz. After full-wave rectification, linear EMG envelopes for the whole duration of each bin of the step cycle were obtained, and the maximal EMG amplitude at each bin across all steps was determined.

The subtracted normalized TA MEPs from each subject was grouped based on the bin number, BWS, and experimental session. The same analysis was conducted for recordings taken from the right soleus muscle based on the overlap of motor cortical representation in humans (Kleinschmidt et al., 1997; Dechent and Frahm, 2003). Statistically significant differences between the mean amplitude of the TA and/or soleus MEPs recorded during stepping from all subjects at 0 BWS and at 25 BWS were established with a Kruskal–Wallis rank-sum test at 2 × 16 or at 2 × 15 levels (2: BWS, 16 or 15: bins) when data were not normally
distributed. When data were normally distributed, a repeated measures analysis of variance (ANOVA) was utilized. Repeated measures ANOVA was conducted to establish statistically significant differences of TA and/or soleus MEPs at 0 and 25 BWS recorded on different experimental sessions, and a Spearman rank order correlation. Bonferroni tests for multiple comparisons were used when a statistically significant difference was detected.

The background EMG activity of the TA muscle at each bin of the step was estimated as the integrated area of the TA EMG linear envelope beginning 80 ms before the TMS pulse for 30 ms, and was normalized to the maximal TA EMG activity. Statistically significant differences between the background EMG activity at 0 and at 25 BWS were established with repeated measures ANOVA. The mean amplitude of the subtracted normalized TA MEPs from each bin of the step was plotted on the \( y \)-axis (dependent variable) against the normalized TA background activity (independent variable) on the \( x \)-axis, and a linear regression line was fitted to the data. This was conducted for each subject at 0 BWS and at 25 BWS as well as for the pooled data from both experimental sessions. The slope and the \( y \)-intercept from the linear regression were evaluated with a Kruskal–Wallis rank sum test for multiple comparisons. In all statistical tests, alpha was set at 0.05. Results are presented as mean values along with the standard error of the mean (SEM), unless otherwise stated.

3. Results

The step duration from all subjects at 0 BWS of the right leg was \( 1.23 \pm 0.04 \) s at session 1 and \( 1.26 \pm 0.04 \) s at session 2. At 25 BWS, the step duration was \( 1.26 \pm 0.04 \) s and \( 1.28 \pm 0.09 \) s for sessions 1 and 2, respectively. No statistical difference was found on the step duration between BWS and sessions \(( P > 0.05)\). The TA MEP latency did not vary with the subjects seated, standing or across sessions (seated: \( 28.32 \pm 0.91 \) ms session 1 and \( 27.99 \pm 1.44 \) ms session 2; standing: \( 28.81 \pm 1.01 \) ms session 1 and \( 27.8 \pm 0.37 \) ms session 2).

3.1. Modulation of TA MEP amplitude during stepping with absent and partial BWS

In Fig. 2, waveform averages of non-rectified TA MEPs from one subject during stepping at 0 BWS (black lines) are shown superimposed on the TA MEPs recorded at 25 BWS (grey lines) for each bin of the step cycle recorded at session 1 (Fig. 2A) and at session 2 (Fig. 2B). The TA EMG activation profiles from this subject during
stepping at 0 and at 25 BWS are shown in Fig. 2C and D, respectively. It is worth noting that the large TA MEP amplitude at heel contact coincided with an increased TA EMG activity from 0% to 5% of the step cycle (Fig. 2C, D), the amplitude of the TA MEPs was not affected when stepping at reduced levels of body loading, and that the modulation pattern was similar for both experimental sessions.

The average normalized amplitude of the TA MEPs from all subjects at each bin of the step cycle at 0 BWS and at 25 BWS for both experimental sessions is indicated in Fig. 2E and F, respectively. At session 1, repeated measures ANOVA showed that the TA MEP amplitude was statistically significant different across bins ($F_{1,14} = 14.95, P < 0.001$) but not between 0 and 25 BWS ($F_{1,14} = 0.1, P = 0.76$). Similarly, the TA MEP amplitude was statistically significant different across bins ($F_{1,15} = 3.97, P < 0.001$) but not between 0 and 25 BWS ($F_{1,15} = 0.15, P = 0.76$) at session 2. The TA MEPs were not statistically significant different between sessions at 0 BWS ($F_{1,14} = 0.33, P = 0.56$) and at 25 BWS ($F_{1,15} = 1.34, P = 0.97$). A correlation coefficient of 0.85 ($n = 193, P < 0.001$) was found for TA MEPs recorded at session 1 and 2.

### 3.2. Modulation of soleus MEP amplitude during stepping with absent and partial BWS

In Fig. 3, waveform averages of non-rectified soleus MEPs during stepping at 0 BWS (black lines) are indicated superimposed on the soleus MEPs recorded at 25 BWS (grey lines) for each bin of the step cycle at 0 BWS (black lines) and at 25 BWS (grey lines) for experimental session 1 (E) and session 2 (F). Grey squares denote the duration of the stance phase. Error bars represent the SEM. BWS = body weight support. MEP = motor evoked potentials.
across sessions ($F_{1,14} = 0.11, P = 0.73$), but it was statistically significant different across bins ($F_{1,14} = 16.1, P < 0.001$). When this analysis was conducted for the soleus MEPS at 25 BWS, a statistically significant difference was found between sessions ($F_{1,14} = 7.06, P = 0.009$). This means that the soleus MEPS at 25 BWS at session 1 were smaller in amplitude compared to those recorded at session 2 (Fig. 3E, F). However, a correlation coefficient of 0.854 ($n = 193$, $P < 0.001$) was found for the soleus MEPS recorded at session 1 and 2.

3.3. Relationship between MEP amplitude and background EMG activity

The TA background EMG activity was not statistically significant different across BWS levels ($F_{1,15} = 0.44, P = 0.5$) and across experimental sessions ($F_{1,15} = 0.11, P = 0.73$), while an interaction between BWS levels and experimental sessions was not found ($P = 0.99$). Similar results were observed for the soleus background EMG activity. A linear relationship between the TA MEP and the TA background EMG activity as well as between the soleus MEP and the soleus background EMG activity was found ($P < 0.001$), regardless of the BWS level or experimental session (Table 1). The slope between TA MEP amplitude and the TA background EMG activity did not vary at 0 and 25 BWS levels ($F_{1,5} = 4.6, P = 0.08$), and experimental sessions ($F_{1,5} = 2.37, P = 0.32$). This was not the case for the y-intercept of the linear regression between the TA MEP amplitude and the TA background EMG activity, in which statistically significant differences were found between sessions ($F_{1,5} > 8.1, P = 0.03$), but not between BWS levels ($F_{1,5} = 1.06, P = 0.34$). Similar results were found for the slope and y-intercept between soleus MEP amplitude and the soleus background EMG activity.

4. Discussion

The principal new findings of this study are that the TA and soleus MEPS are modulated in a phase-dependent pattern under conditions of full and partial body weight loading during stepping in healthy humans. Further, the amplitude modulation of the TA and soleus MEPS did not vary when recorded at different experimental sessions in the same subjects.

The TA MEPS were profoundly increased at heel contact and progressively decreased until late stance, followed by a significant facilitation at swing phase initiation (bin 9) that remained throughout the swing phase regardless of the BWS level or session (Fig. 2). At swing-to-stance transition phase (bin 16) the TA MEP amplitude was similar to that observed at heel contact (Fig. 2). In contrast, the soleus MEP was progressively increased during the stance phase reaching maximal amplitude at late-stance phase (bin 8; Fig. 3E, F) when the TA MEP reached its smallest amplitude (Fig. 2). The soleus MEP amplitude was decreased during swing phase initiation and remained decreased throughout the swing phase regardless of the BWS level or session (Fig. 3). These findings are consistent to those reported in humans during stepping without BWS (Schubert et al., 1997; Capaday et al., 1999). The TA MEPS during the transition from stance to swing were smaller compared to the MEPS elicited during the period of flexor activity (Capaday et al., 1999), a behavior we also observed in this study (see bin 8 in Fig. 2).

The slope of the linear regression between TA/soleus MEPS amplitude with the associated background EMG activity did not vary across BWS levels or experimental sessions (Table 1). However, the y-intercepts for the TA MEPS were decreased and for the soleus MEPS were increased at session 2 compared to session 1 (Table 1), suggesting for excitability changes across sessions. The MEP amplitude is related to the background EMG activity level, while at increased levels of motor activity (stance vs. swing phase) its amplitude depends on the size of the initial compound muscle action potential (Capaday, 1997). However, both background EMG activity and MEP thresholds did not vary across BWS levels and experimental sessions. The increased y-intercept can partly explain the increased soleus MEP amplitudes recorded at session 2 during stepping at 25 BWS. Given the limitations of the current experimental protocol, we can only assume that differences in the y-intercept may be due to intrinsic neuronal characteristics of corticomotoneuronal cells related to the non-linear relationship between MEP size and background activity.

During robotic air stepping (100 BWS), the TA MEP amplitude was significantly reduced at early-stance and mid-swing phases when compared to that observed at 0 BWS (Kamibayashi et al., 2009). The overall TA MEP modulation pattern was somewhat different from what we observed here (compare Fig. 2 with Fig. 3 in Kamibayashi et al., 2009), since TA MEP depression from mid to late stance and TA MEP facilitation throughout the swing phase were absent in the study of Kamibayashi and colleagues (Kamibayashi et al., 2009). Differences between the TA MEPS amplitudes at 0 BWS and our findings can be attributed to differences in the methodology employed, including but not limited to the resolution of the step cycle, treadmill speed, and to the robotic-driven leg movements during walking.

At this point, we should consider whether the TMS-induced MEPS during walking are a mere reflection of the ongoing locomotor EMG activity. In this study, we found that both the TA and soleus MEPS at 0 BWS and at 25 BWS were linearly related to the associated background EMG activity (Table 1), consistent to findings reported elsewhere (Capaday et al., 1999). However, it should be noted that the TA MEP was progressively decreased during the stance phase when the homologous EMG was quiescent, and the soleus MEP increased at swing-to-stance transition phase when the soleus EMG was quiescent (Figs. 2 and 3). Because the MEPS are not influenced by changes in presynaptic inhibition (Nielsen et al., 1999), the differential modulation of EMG and MEPS at these events of the step cycle might be related to actions of spinal inhibitory interneuronal circuits activated by the corticospinal volley.

MEPS are the result of synchronous motor unit potentials in response to indirect and direct waves arriving onto spinal motoneurons (Devanne et al., 1997; Di Lazzaro et al., 2008). TMS at 1.2 MEP

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<th>Table 1</th>
<th>Linear relationship between MEPS and background EMG activity during walking with absent and partial BWS.</th>
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<td>Tibialis anterior MEPS</td>
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<td>Session 1</td>
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<tr>
<td>Slope</td>
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<tr>
<td>Intercept</td>
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<td>$R^2$ (P-value)</td>
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<tr>
<td>Intercept</td>
<td>+1.60</td>
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<td>$R^2$ (P-value)</td>
<td>0.95 (0.001)</td>
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* Linear regression analysis conducted between the normalized subtracted TA MEP and normalized TA background EMG activity and between the normalized subtracted soleus MEP and normalized soleus background EMG activity. P-values in parentheses are the results from the regression analysis of variance. BWS = body weight support. MEP = motor evoked potentials.
resting threshold created multiple descending volleys, which probably activated corticometoneuronal cells projecting directly to the agonist motoneuronal pool as well as corticospinal cells projecting to the antagonist motoneuron pool and spinal inhibitory interneurons. The amplitude modulation of the TA and soleus MEPs we observed here was partly mediated by changes in the excitability of corticospinal cells with direct monosynaptic connections to the spinal motoneurons (Petersen et al., 1998). Since the excitability pattern of the TA and soleus MEPs was in an opposite direction, we suggest that corticospinal excitatory postsynaptic potentials might have been exerted on mutual spinal inhibitory interneuronal circuits.

One of the gait rehabilitation approaches in neurological disorders (stroke and spinal cord injury) involves training on a motorized treadmill with a harness-lift system that provides partial BWS (Barbeau et al., 1987; Visentin et al., 1998; Pohl et al., 2002; Knikou, 2013). The similarities we observed on the modulation pattern of the MEPs to those reported during human walking without BWS, suggest that cortical control of spinal interneuronal circuits engaged in patterned motor activity are not affected when sensory feedback related to body loading is reduced. Thus, based on our findings it is clear that treadmill walking with an upper body harness that provides partial BWS preserves corticospinal commands in humans. It remains to be shown to what extent corticospinal excitability is impaired in neurological disorders during stepping with absent or reduced BWS.

5. Limitations

The amplitude modulation of the MEPs was examined at 25 BWS and not at higher levels of BWS, because the soleus H-reflex excitability during BWS assisted stepping in healthy humans is not affected by the level of the BWS (Knikou et al., 2009a, 2011). Corticospinal excitability, however, should be further examined at different BWS levels and treadmill speeds as well as at multiple points of the ascending portion of the MEP input–output curve (Capaday et al., 1999; Capaday, 1997). The latter will quantify whether small and large polysynaptic MEPs are modulated different or similar during BWS-assisted stepping in humans. Last, the soleus MEPs were recorded when the motor hot spot was optimal for the TA muscle and not for the soleus muscle. However, since TMS can mimic the natural activation of the M1 (Gentner and Classen, 2006), and activation of limb muscles appear to involve common motor cortical circuits (Devanne et al., 2002), multi-muscle recordings can provide valuable information on excitability changes for antagonistic and/or synergistic muscles at a given motor task.

6. Conclusion

Human locomotion is regulated by supraspinal centers, spinal neuronal networks, and sensory afferent feedback (Knikou, 2010; Barthélémy et al., 2011). The phase-dependent amplitude modulation of the TA and soleus MEPs we observed here is tightly coupled to the neural control of human locomotion. Our findings provide evidence that under conditions of reduced body loading the strength of corticomotoneuronal drive is not altered. Based on our results, we propose that retraining of gait in neurological disorders at reduced levels of body loading does not change the strength of corticospinal drive, and thus it will not negatively affect interactions between corticospinal and spinal neuronal pathways.

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