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CORTICAL CONTROL OF ANTICIPATORY POSTURAL ADJUSTMENTS PRIOR TO STEPPING

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Abstract—Human bipedal balance control is achieved either reactively or predictively by a distributed network of neural areas within the central nervous system with a potential role for cerebral cortex. While the role of the cortex in reactive balance has been widely explored, only few studies have addressed the cortical activations related to predictive balance control. The present study investigated the cortical activations related to the preparation and execution of anticipatory postural adjustment (APA) that precede a step. This study also examined whether the preparatory cortical activations related to a specific movement is dependent on the context of control (postural component vs. focal component). Ground reaction forces and electroencephalographic (EEG) data were recorded from 14 healthy adults while they performed lateral weight shift and lateral stepping with and without initially preloading their weight to the stance leg. EEG analysis revealed that there were distinct movement-related potentials (MRPs) with concurrent event-related desynchronization (ERD) of mu and beta rhythms prior to the onset of APA and also to the onset of foot-off during lateral stepping in the fronto-central cortical areas. Also, the MRPs and ERD prior to the onset of APA and onset of lateral weight shift were not significantly different suggesting the comparable cortical activations for the generation of postural and focal movements. The present study reveals the occurrence of cortical activation prior to the execution of an APA that precedes a step. Importantly, this cortical activity appears independent of the context of the movement.

Key words: stepping, balance control, anticipatory postural adjustments, readiness potential, supplementary motor area, event-related desynchronization.

INTRODUCTION

Human bipedal balance control is a remarkable complex sensorimotor mechanism which is controlled both reactively and predictively by the central nervous system (CNS). While reactive balance control compensates for unpredictable postural perturbations, predictive (anticipatory) balance control minimizes the destabilizing effect of predictable perturbations and voluntary movements (Massion, 1992; Maki and McIlroy, 1997; Jacobs and Horak, 2007). For instance, prior to stepping, it is necessary to transfer the center of mass (COM) laterally to the stance leg in order to maintain equilibrium. This lateral weight shift, which is also referred to as mediolateral (ML) anticipatory postural adjustment (APA), involves an initial increase in vertical loading on the swing leg with a concurrent ML center of pressure (COP) displacement toward this leg to propel the COM toward the stance limb (Halliday et al., 1998; McIlroy and Maki, 1999). The APA (e.g., lateral weight shift) and focal movement (e.g., stepping) must be coordinated by the CNS in order to achieve the desired movement while also maintaining stability. The focus of the present study is to advance the understanding of the cortical contributions to balance control with specific attention to anticipatory control during stepping.

It has been proposed that a distributed neural network including cerebellum, basal ganglia, thalamus, and cortex are involved in the generation and execution of APA (Massion, 1984, 1992; Ng et al., 2011). During gait initiation, parkinsonian patients and cerebellar patients display APA impairments including decreased force production, reduced COP excursion, delayed APA execution, and prolonged anticipatory phase. These impairments reveal the potential role of basal ganglia and cerebellum in APA (Burleigh-Jacobs et al., 1997; Timmann and Horak, 2001). Clinical studies that examined the location of brain damage and impairment of APAs associated with rapid arm raising, bimanual load lifting (BMLL), leg lift, and step initiation suggested a potential role for premotor cortex, supplementary motor area (SMA), and primary motor cortex (M1) in the generation and execution of APA (Gurfinkel and Elner, 1988; Birjukova et al., 1989; Massion, 1992; MacKinnon et al., 2007; Yakovenko and Drew, 2009; Chang et al., 2010). Magnetoencephalographic (MEG)

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Abbreviations: AP, anteroposterior; APA, anticipatory postural adjustment; BMLL, bimanual load lifting; CNS, central nervous system; COM, center of mass; COP, center of pressure; EEG, electroencephalographic; EOG, electrooculographic; ERD, event-related desynchronization; ERSPs, event-related spectral perturbations; ICA, independent component analysis; M1, primary motor cortex; MEG, magnetoencephalographic; ML, mediolateral; MMP, movement-monitoring potential; MP, motor potential; MRPs, movement-related potentials; NS, negative slope; RP, readiness potential; SMA, supplementary motor area.

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studies of APAs during the BMLL task in healthy adults also showed activation associated with the SMA and M1 (Ng et al., 2011, 2013).

Electroencephalographic (EEG) studies have revealed the cortical activations associated with APA during voluntary movements in both frequency and voltage domains as event-related desynchronization (ERD) of mu and beta rhythms and movement-related potentials (MRPs), respectively. APA during the BMLL task (reduction in the biceps brachii muscle activity of the load-bearing arm) was associated with an ERD of mu (8–13 Hz) and central beta rhythms (16–30 Hz) over M1 and SMA (Barlaam et al., 2011; Ng et al., 2011). MRPs preceded the onset of APA during voluntary rising on tiptoes with maximum amplitude over Cz (Saitou et al., 1996). A late CNV wave related to APAs during gait initiation and during bilateral shoulder flexion while standing was also reported using CNV paradigms (Yazawa et al., 1997; Maeda and Fujiwara, 2007). These studies all appear to point to an important role for fronto-central cortical sites for the execution of APA; however, in many of these studies it is difficult to disentangle the cortical activity that maybe linked to the APA and the concurrent or subsequent focal movement. For example, in forward stepping while the ML APA is being executed the CNS is concurrently generating force to cause anteroposterior (AP) instability (i.e., to move the COM forward for stepping). In arm raise studies, the timing between the onset of the APA and the onset of arm movement can be quite compressed making it difficult to separate them temporally. As a result, in many tasks studied, the APA phase may be temporally entangled with the control of the focal task.

To better understand the potential role of cortical activity for the predictive postural elements it is necessary to isolate the APA phase from the focal task. Yoshida et al. (2008) isolated the APA-related component in MRPs by comparing unilateral shoulder flexion movements while standing and sitting. They found increased amplitude on all three components of the MRPs (readiness potential (RP), motor potential (MP), and movement-monitoring potential (MMP)) in the standing condition. Ng et al. (2013) isolated the APA in the BMLL task by comparing with a control task that has no APA and found ERD of beta rhythm associated with APA over the sensorimotor cortical areas. The challenge in gait initiation or forward stepping, as noted, is that the period of control that encompasses the APA is composed of two elements: (1) the APA involving the ML motion of the COM prior to limb unloading and (2) the AP movement of the COM to advance the body forward for a forward step. In this way the cortical control of the events prior to unloading are comprised of a predictive balance component and the focal task of moving forward. To better isolate the ML APA the current study explores laterally directed stepping removing concurrent control of the ML APA and the focal AP movement.

The present study advances the understanding of the cortical involvement in the control of anticipatory balance control. The primary objective of this study was to isolate cortical activity related to the preparation of an APA. To do this we examined the cortical events prior to the ML APA preceding a lateral stepping task. To isolate the cortical activity specifically associated with the execution of an APA, we compared the cortical events prior to the focal task of lateral stepping between conditions with and without a preceding APA (i.e., the limb is unweighted prior to stepping reducing the need for an ML APA). An additional objective was to determine if observed APA-related cortical activity was unique to the performance of a movement as part of an APA or, rather, was comparable to execution of the same movement as part of a focal task. To address this objective, we compared the pre-motor cortical events of an ML APA that automatically precedes lateral stepping with a voluntary ML weight shift that was not associated with any stepping reaction.

EXPERIMENTAL PROCEDURES

Participants

Fourteen healthy volunteers (19–33 years, three females) participated in this study. No subjects reported any history of neuromuscular or CNS disorders. The experimental procedures were performed in accordance with the declaration of Helsinki and approved by the Research Ethics Board of the University of Waterloo. Prior to the experiment, the subjects were given a description of the study and each participant provided written informed consent.

Experimental design

Participants stood barefoot with each foot on one of the two force plates with arms by their sides and eyes open. They selected a comfortable stance width (approximately shoulder width) and the outline of their feet was traced using tape markers to maintain the same starting foot position throughout the experiment. Subjects fixed their gaze on a cross sign placed at eye level on the wall in front of them and maintained that gaze while performing the task.

Participants performed the following three motor tasks in response to an auditory cue: (1) equal-weighted lateral stepping (stepping preceded by APA), (2) unloaded lateral stepping (stepping with no APA) and (3) lateral weight shift (APA-like movement without the subsequent step). Four blocks of trials were performed for each of the three tasks for a total of 12 blocks. The order of these blocks was randomized. Each block consisted of 10 trials for a total of 120 trials (i.e., 40 trials for each task). In equal-weighted lateral stepping, participants initially stood on the force plate with equal weight over each limb and responded to the auditory cue by quickly stepping laterally with their right leg over a rectangular foam barrier placed to their right. The use of a foam barrier standardized the stepping height required in stepping tasks and also ensured an APA phase with sufficient amplitude in equal-weighted lateral stepping. In unloaded lateral stepping, participants initially stood with their body weight transferred over the left leg to unload the right leg while keeping it in contact with the

ground. They remained in that position until, upon hearing the auditory cue, they stepped over the foam barrier with their right leg. Thus, in unloaded lateral stepping there was no APA phase. After the stepping trials, subjects returned to the initial stance position at their own pace. In the lateral weight shift task, participants initially stood on the force plate with equal weight over each limb. Upon the auditory cue they performed a quick weight transfer to the left leg and returned to the initial stance position at their own pace. They were allowed to rest between blocks and practice trials were given prior to data collection.

Data acquisition

Postural data. Vertical and horizontal ground reaction forces and corresponding moments from two force plates (AMTI model OR 6–5, Watertown, MA, USA) that were positioned side by side were recorded using a custom-built LabVIEW (National Instruments, TX, USA) program. Prior to data collection, the force plates were calibrated with the foam barrier on the right force plate. During the experiment, force plate signals were monitored online especially in the unloaded stepping trials to ensure the absence of APA. Unloaded stepping trials that contained an APA phase were discarded from further analysis. Force plate data were amplified (gain: 1000), analog low-pass filtered using two-pole low-pass 1000-Hz filter (built in AMTI MSA-6 MiniAmp amplifier), sampled online at a rate of 1000 Hz, and stored for subsequent analysis.

EEG data. EEG data were acquired online using 32 Ag/AgCl electrodes mounted on a cap (Quick-cap, Compumedics Neuroscan, USA) and Neuroscan 4.3 software. Electrooculographic (EOG) signals were also recorded using four EOG electrodes positioned above and below the left eye and lateral to the outer canthi of both eyes. The impedances of all EEG and EOG electrodes were kept below 5 KΩ throughout the experiment and they were referenced to linked mastoids. The acquired EEG signals were amplified (gain: 19), sampled (1000 Hz), filtered (DC-260 Hz) online using 40-channel digital EEG amplifier (Nuamps, Compumedics Neuroscan, USA), and then stored for offline analysis.

Data analysis

Postural data. Post-processing of force plate data (using a custom-built LabVIEW program) included low-pass filtering (6-Hz, dual-pass 2nd-order Butterworth filter), ML COP calculation, feature extraction, and writing event files that contain the time points of APA and FO onset. These event files were later used to mark the APA and FO time points on EEG data. Since the APA phase of equal-weighted lateral stepping consist of a lateral weight shift, we used the term 'APA onset' to refer the onset of lateral weight shift (in terms of ML COP displacement) in both equal-weighted stepping and lateral weight shift tasks. All latencies were expressed with respect to the onset of the auditory cue. Reaction time was expressed as the APA onset for lateral weight shift and equal-weighted stepping and the onset of unloading for unloaded stepping. These onsets were defined as the time points when the ML COP displacement toward the right limb deviated by 4 mm from the mean baseline ML COP (baseline was calculated over a time window of 200 ms after the auditory cue). The onset of unloading for equal-weighted stepping was the time of peak APA (peak amplitude of ML COP excursion toward the right limb). The onset of stepping was defined as the onset of APA for equal-weighted stepping and the onset of unloading for unloaded stepping. Magnitude of APA was expressed as the peak APA amplitude relative to the mean baseline ML COP. Time to peak APA was the time of peak amplitude of ML COP excursion toward the right limb. Duration to peak APA was measured from the onset of APA until time to peak APA. The onset of FO was defined to be the time when the loading on the right force plate dropped to less than 1% of the body weight. The time required to unload the swing foot (unloading phase duration) for both stepping tasks was measured from the onset of unloading until the onset of FO. Total stepping time was defined as the time between onset of FO and onset of stepping (McIlroy and Maki, 1993, 1996, 1999; Zettel et al., 2002; Lakhani et al., 2011).

EEG data. Offline analyses of EEG data were performed in MATLAB (The Mathworks, Natick, MA, USA) using custom-made scripts written to run in EEGLAB v13.0.1 (Delorme and Makeig, 2004). EEG data were band pass filtered (0.05–50 Hz), segmented into 3-s epochs with respect to APA and FO onsets (1.5 s before and after the trigger points), and baseline corrected (baseline period: −1.2 s to −1 s). Ocular, muscular, cardiac, movement, and line noise artifacts were eliminated using independent component analysis (ICA). One of the major artifacts that can encounter in stepping studies is the movement artifact (Thompson et al., 2008); however, ICA has been used to remove movement artifacts (Thompson et al., 2008; Gwin et al., 2011; Wagner et al., 2012). ICA decomposes the multi-channel EEG data into spatially fixed and temporally independent components statistically without prior knowledge about the signal and noise components in the input EEG data (blind source separation) thereby separating the contributions of brain sources and artifactual sources (Bell and Sejnowski, 1995; Makeig et al., 1996, 1997; Jung et al., 1998; Delorme et al., 2002). The ICA pruned epoched data were once again visually inspected and any additional noisy epochs were rejected manually.

MRPs related to APA and FO were obtained by grand averaging (n = 14) the individual-averaged epochs that were time-locked to the onset of APA and FO, respectively. MRP waveform morphology and topographic voltage maps were characterized using the grand-averaged data. The peak amplitudes of specific components within MRPs related to both APA and FO were extracted from averaged single-subject data for each condition as follows: (1) the peak negativity of the

RP measured between −600 ms and −500 ms, (2) the peak negativity of the MP measured between −100 ms and 0 ms, and (3) the negative slope (NS) by subtracting the RP amplitude from MP amplitude (Singh et al., 1992; do Nascimento et al., 2005; Yoshida et al., 2008). For equal-weighted stepping and lateral weight shift, the amplitude of MMP was also measured which is defined as the peak negativity between 0 ms and time of peak APA. The topographic voltage maps were plotted at discrete time points to visualize the scalp distribution of MRPs related to APA and FO. Brain ICs that contributed to the MRPs were selected based on the percentage of power contributed to the grand-averaged waveform.

In the frequency domain, the spectral power changes were characterized in terms of event-related spectral perturbations (ERSPs), which is a generalization of ERD. The ERSP computes the mean log event-related spectral power changes relative to a mean pre-event baseline spectra using Morlet wavelet transform techniques and plots the spectral changes at discrete frequencies as a function of time (Makeig, 1993; Delorme and Makeig, 2004; Roach and Mathalon, 2008). Both ERP and ERSP analysis were focused on mid fronto-central electrodes.

Statistical analysis

Two-tailed paired *t*-tests were used to assess the significant differences ($p < .05$) in the postural and EEG dynamics related to APA (between lateral weight shift and equal-weighted stepping) and FO (between equal-weighted stepping and unloaded stepping).

RESULTS

Movement characteristics

All 14 participants performed the three task conditions with a mean reaction time of 290 ± 41 ms (mean ± SD), 270 ± 42 ms, and 309 ± 55 ms for lateral weight shift, equal-weighted lateral stepping, and unloaded lateral stepping, respectively. Example of single-trial responses for each task condition is provided in Fig. 1. As instructed, participants stood initially with equal weight on both legs for lateral weight shift (baseline ML COP: −0.02 ± 0.02 m) and equal-weighted stepping (baseline ML COP: −0.03 ± 0.03 m) and preloaded their weight to the left leg in unloaded stepping (baseline ML COP: −0.15 ± 0.05 m). The magnitude of APA did not differ between task conditions (lateral weight shift: 0.077 ± 0.02 m; equal-weighted stepping: 0.078 ± 0.02 m; $t_{14} = -0.09$, $p = .93$). However, the duration to peak APA was significantly shorter for equal-weighted stepping than lateral weight shift (197 ± 49 ms vs. 248 ± 40 ms; $t_{14} = 6.86$, $p < .05$). The presence of the APA phase significantly delayed the onset of FO for equal-weighted stepping compared to unloaded stepping (661 ± 94 ms vs. 384 ± 64 ms; $t_{14} = 13.15$, $p < .05$). Subsequently, the unloading phase duration (193 ± 30 ms vs. 76 ± 23 ms; $t_{14} = 10.63$, $p < .05$) and total stepping time (390. 83 ± 69 ms vs. 76 ± 23 ms; $t_{14} = 16.01$, $p < .05$) were also significantly greater for equal-weighted stepping compared to those of unloaded stepping.

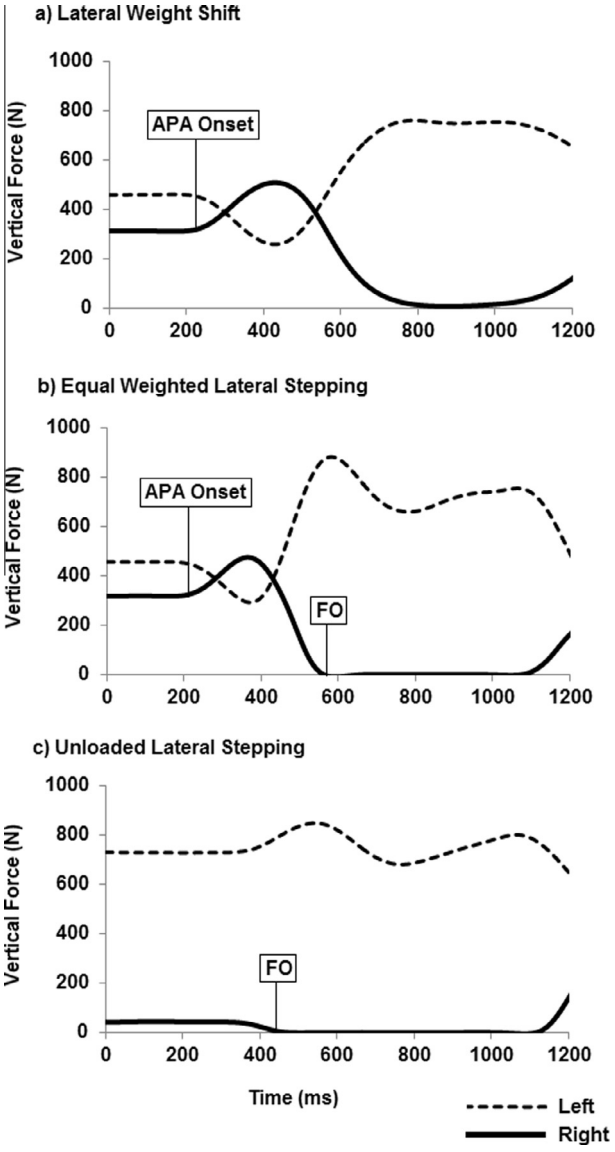

Fig. 1. Example of single-trial responses. Vertical ground reaction forces under the swing (solid line) and stance (broken line) foot for lateral weight shift (a), equal-weighted lateral stepping (b), and unloaded lateral stepping (c). Time 0 indicates the onset of auditory cue. The trials were selected, at random, from a single subject. The onset of lateral weight shift is labeled as APA Onset for lateral weight shift condition and equal-weighted lateral stepping. The onset of foot-off is labeled as FO for equal-weighted lateral stepping and unloaded lateral stepping. Note that there is no FO in the lateral weight shift condition and no APA in the unloaded lateral stepping.

MRPs

Fig. 2 illustrates the grand-averaged ($n = 14$) MRPs related to APA and FO at Cz electrode site. The MRPs had maximum amplitude at Cz electrode, hence further analysis was focused on the Cz electrode. The grand-averaged plot (Fig. 2a) revealed that there is a specific MRP related to the preparation and execution of APA with no significant difference between lateral weight shift

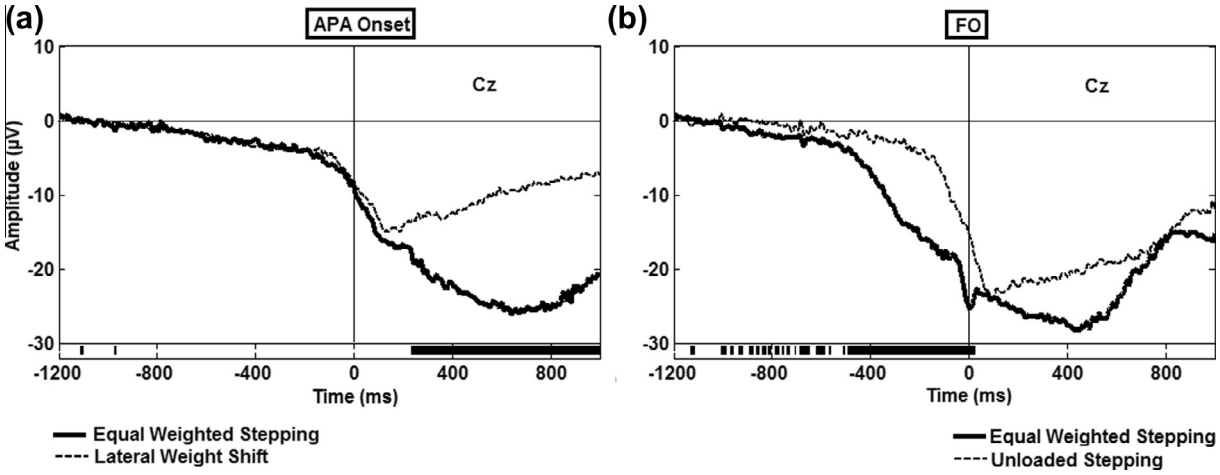

Fig. 2. MRPs at Cz electrode. Grand-averaged (n = 14) MRPs of equal-weighted lateral stepping (solid line) and lateral weight shift (broken line) epoched around (t = 0) APA onset (a) and foot-off onset (b). Black rectangles under the MRP plots indicate regions of significant (p < .05) differences in MRP amplitudes between task conditions.

and equal-weighted stepping for peak amplitude of RP, MP, NS, and MMP (Table 1). In addition, a paired t-test performed at each time point also showed no significant difference (p > .05) in the MRP related to APA between lateral weight shift and equal-weighted stepping. The grand-averaged plot of MRP related to FO (Fig. 2b) revealed that there is a specific MRP related to the preparation and execution of FO, which differed significantly between equal-weighted stepping and unloaded stepping for peak amplitude of MP and NS (Table 1). However, even though the RP amplitude of equal weighed stepping was greater than that of unloaded stepping, this difference was not statistically significant (Table 1). The paired t-test performed at each time point also showed a significant difference (p < .05) in the MRPs prior to FO between equal-weighted stepping and unloaded stepping. The topographic maps plotted at the different time points before and after APA and FO onset are shown in Fig. 3. RP related to APA begins approximately 800 ms prior to the onset of APA and is localized to mid-central areas, whereas MP and MMP are widely distributed over the fronto-central-parietal areas.

ERSPs

The grand-averaged ERSP plots at the Cz electrode are depicted in Fig. 4. ERSP analysis revealed the power spectral changes at specific frequencies (3–50 Hz) and time points relative to the onset of APA and FO. The time–frequency analysis of MRP related to APA during lateral weight shift and equal-weighted stepping (Fig. 4a, b) revealed a robust mu ERD and phasic beta ERD during RP with no significant difference in spectral power between two task conditions (p > .05). This ERD was followed by mu ERS which started approximately 200 ms prior to the APA onset and lasted until the end of APA for lateral weight shift and until the FO for equal-weighted stepping. The time–frequency analysis of MRP related to FO during equal-weighted and unloaded stepping (Fig. 4c, d) also showed mu and beta ERD during RP with no significant difference between the two task conditions (p > .05). For unloaded stepping this ERD was followed by robust mu ERS and phasic beta ERS which started approximately 200 ms prior to the onset of FO. However, for the equal-weighted stepping the ERS started around 400 ms prior to the FO onset (this early ERS corresponds to the ERS that occurred during APA) and there was a robust mu and beta ERS during MP which was significantly different (p < .05) than that of unloaded stepping. A phasic gamma ERS (30–40 Hz) was also observable during RP for both APA- and FO-related MRPs.

Movement-related ICs

The brain ICs were identified based on the amount of power they contributed to the generation of the MRP

Table 1. Peak amplitudes of movement-related potentials related to APA and FO

	APA			FO		
	Lateral weight shift (μV)	Equal-weighted stepping (μV)	p value	Equal-weighted stepping (μV)	Unloaded stepping (μV)	p value
RP	−4.10 ± 3.31	−4.39 ± 3.41	.77	−5.43 ± 3.71	−4.54 ± 2.74	.33
MP	−9.19 ± 7.82	−10.96 ± 9.08	.20	−26.43 ± 14.11	−17.19 ± 13.16	< .05
NS	−5.09 ± 6.04	−6.57 ± 6.54	.06	−21.00 ± 11.21	−12.17 ± 11.24	< .05
MMP	−16.92 ± 11.67	−18.56 ± 11.50	.36			

Grand-averaged (n = 14) MRP amplitude values at Cz are presented as mean ± standard deviation. RP: readiness potential, MP: motor potential, NS: negative slope, and MMP: movement-monitoring potential. MMP values were measured only for MRPs related to APA.

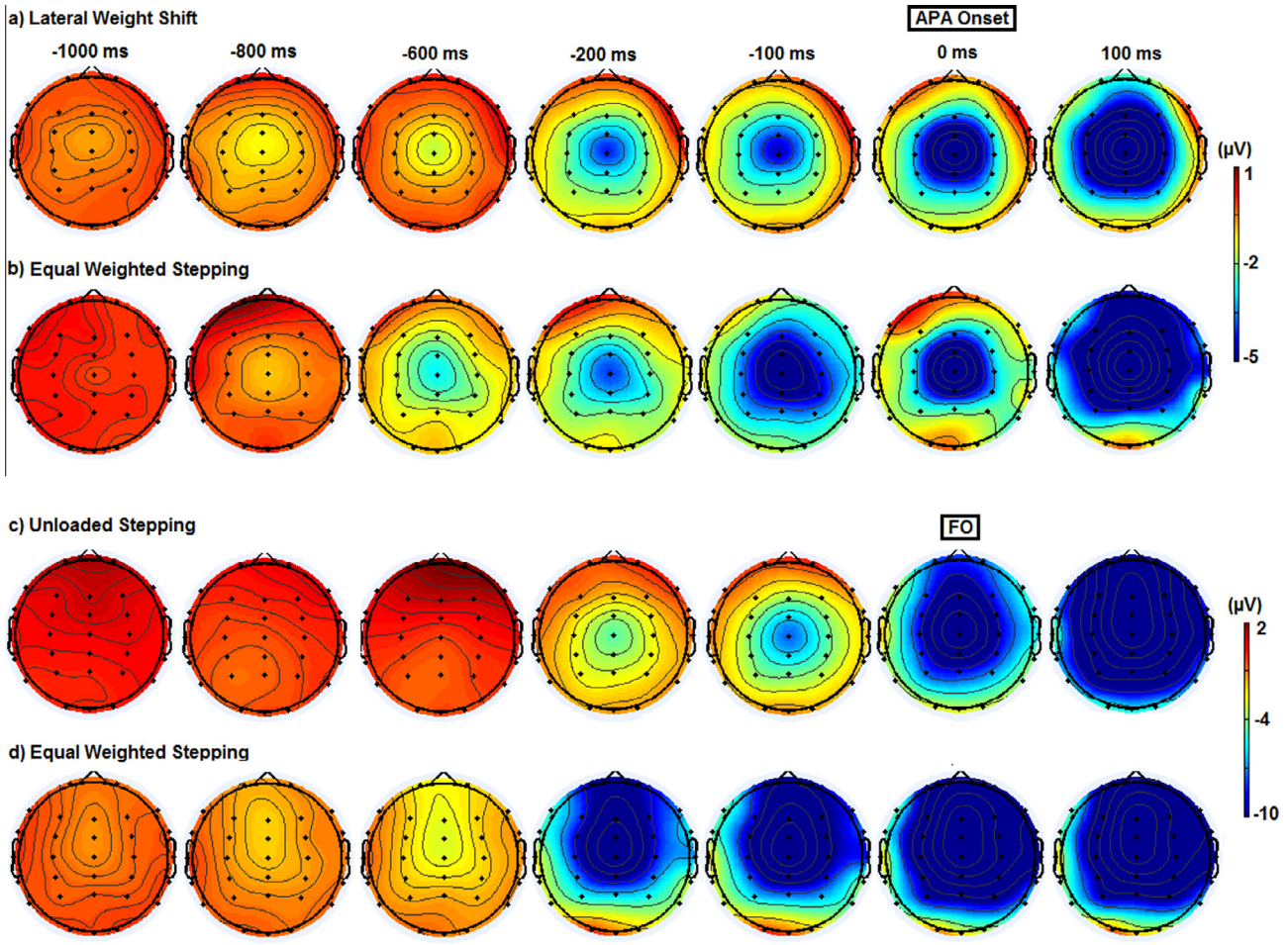

Fig. 3. Scalp topographies of MRPs. Topographic voltage maps of grand-averaged MRPs ($n = 14$) related to APA (0 ms denotes the onset of APA) at different time points during lateral weight shift (a) and equal-weighted stepping (b). Topographic voltage maps of grand-averaged MRPs ($n = 14$) related to FO (0 ms denotes the onset of FO) at different time points during equal-weighted stepping (c) and unloaded stepping (d). Color scales depict MRP amplitudes in microvolts and black dots depict the electrode locations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Delorme and Makeig, 2004). Component scalp maps of the brain ICs that show relative projection strength and time course of activity are provided in Fig. 5. The scalp topography of the brain ICs of all MRPs demonstrated a mid fronto-central activation. The component activity of the brain ICs resembled that of the Cz electrode activity.

DISCUSSION

To our knowledge, this is the first study to explicitly examine the cortical activity related to the preparation of an APA prior to stepping using ERP and time–frequency analysis. The results were highlighted by discrete cortical events in the voltage and frequency domain linked to APA and FO during lateral stepping.

MRPs

In the present study, the MRPs measured prior to the APA that preceded equal-weighted stepping was similar to the MRPs measured prior to the execution of a lateral weight shift. By having participants step laterally, we were able to isolate the MRPs that are solely related to the generation of ML APA. In our lateral stepping task, the anticipatory control occurred prior to the voluntary step unlike voluntary forward stepping where the lateral anticipatory control occurs concurrent with the AP advancement of the COM for the purpose of forward progression (McIlroy and Maki, 1993; Halliday et al., 1998). As such, we were able to isolate RPs and MPs specifically related to the APA and not the focal stepping task. RPs during voluntary movements begin 0.8–1.5 s prior to movement onset and are distributed bilaterally over frontal, central, and parietal areas with maximum amplitude at vertex (Cz) (Kornhuber and Deecke, 1965; Vaughan et al., 1968; Deecke et al., 1976; Boschert et al., 1983; Lang et al., 1991; Jahanshahi et al., 1995). It is suggested that the RP reflects the facilitatory events in the dendritic network of those cortical areas related to the preparation of movement (Gilden et al., 1966; Vaughan et al., 1968; Deecke et al., 1976). In addition, lesion studies, intracranial recordings, and source localization studies have shown that RP arises from SMA and M1 (Vaughan et al., 1968; Deecke et al., 1976; Boschert et al., 1983; Lang et al., 1991; Ikeda et al., 1992). MPs have been

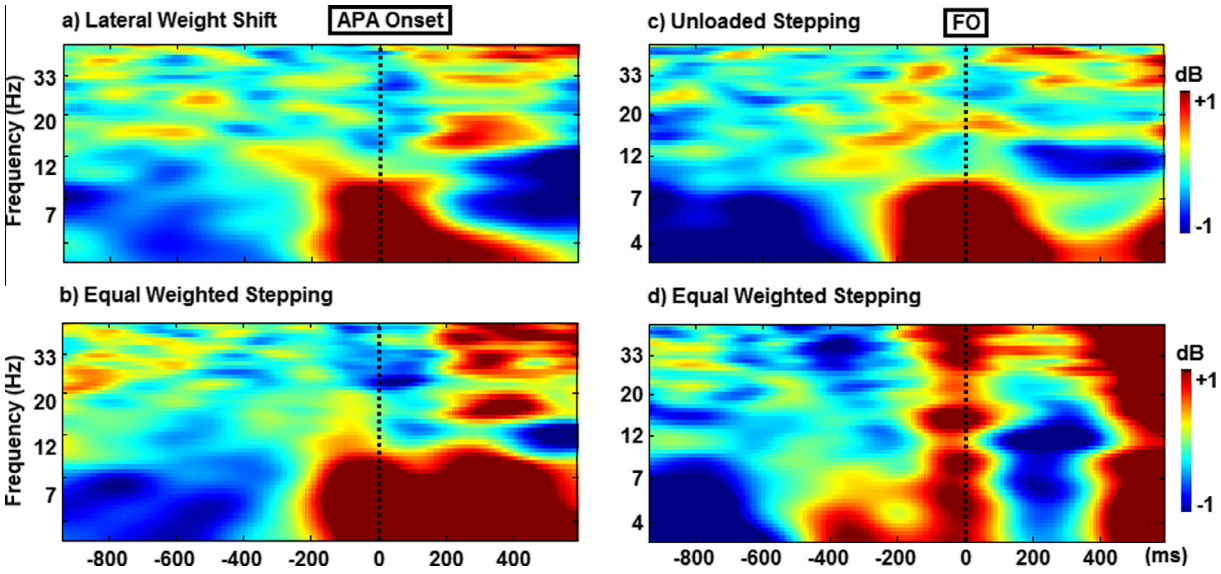

Fig. 4. ERSP Plots. Time–frequency maps of grand-averaged (n = 14) MRPs related to APA (0 ms denotes the onset of APA) during lateral weight shift (a) and equal-weighted stepping (b). Time–frequency maps of grand-averaged (n = 14) MRPs related to FO (0 ms denotes the onset of FO) during equal-weighted stepping (c) and unloaded stepping (d). Color scale depicts the spectral power of MRPs in decibels. Blue color indicates an event-related desynchronization whereas red color indicates an event-related synchronization. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

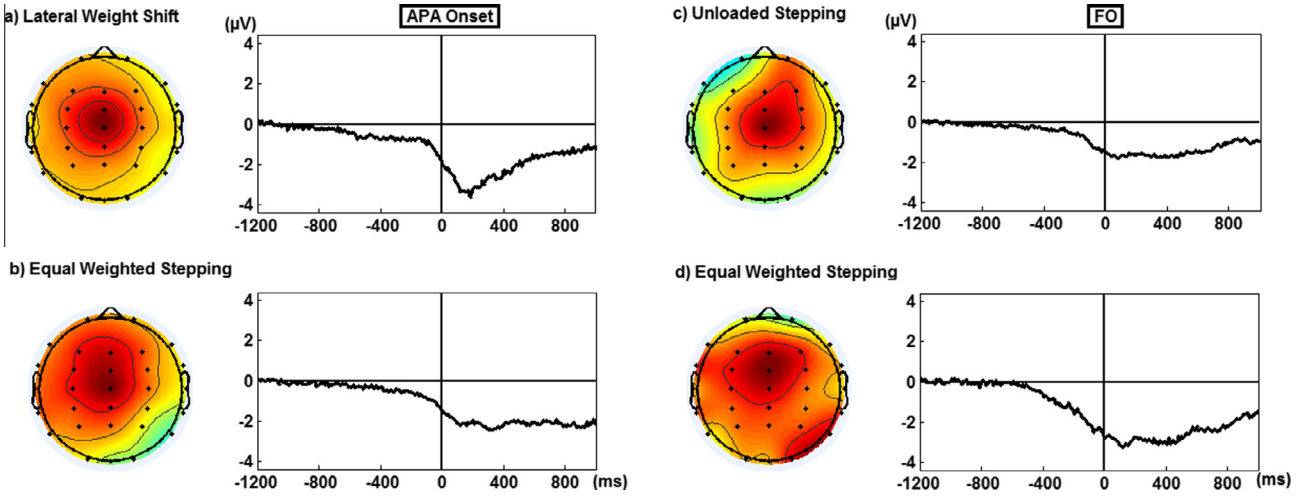

Fig. 5. MRP-related ICs. Scalp maps (left frame) and time course of activity (right frame) of the independent components that contributed maximum power to the MRPs related to APA (0 ms denotes the onset of APA) during lateral weight shift (a) and equal-weighted stepping (b). Scalp maps (left frame) and time course of activity (right frame) of the independent components that contributed maximum power to the MRPs related to FO (0 ms denotes the onset of FO) during equal-weighted stepping (c) and unloaded stepping (d).

shown to start 50–100 ms prior to the movement onset and have maximum amplitude over the vertex for voluntary foot movements (Gilden et al., 1966; Deecke et al., 1976; Ikeda et al., 1992). MP reflects the synaptic potentials related to the pyramidal tract neuronal discharge in the motor cortex (Gilden et al., 1966; Deecke et al., 1976; Ikeda et al., 1992). Thus, it is proposed that the MRPs are indicators of cortical activation, which is a combination of decreased membrane potential and increased excitatory post synaptic potentials (EPSPs) of cortical cells (Gilden et al., 1966; Deecke et al., 1976). In the present study, the characteristics of the RPs and MPs observed prior to the APA onset are in line with RP and MP characteristics from these previous studies. The present results emphasize the important role of the cortex in anticipatory balance control even when it is automatic.

The postural results revealed that the magnitude of APA did not differ between voluntary lateral weight shift and the automatic response that precedes equal-weighted stepping. Hence, it might be possible that the CNS controls the APA as a sequentially independent movement separate from the limb unloading associated with the step phase. Previous studies have shown the existence of MRPs prior to the APA in addition to the MRPs prior to the focal task during voluntary rising on tip toes (Saitou et al., 1996). The authors concluded that the CNS relies on separate motor programs to generate APA and focal movement as suggested by Nardone and

Schieppati (1988). In addition, during a BMLL task, Barlaam et al. (2011) reported a negative wave over the left M1 hand area and a simultaneous positive wave over the right M1 hand area. The authors interpreted these results as evidence of a separate postural command that generates the APA (inhibition of the postural muscle activity as reflected by the positive wave over the contralateral M1 of postural arm) and motor command that generates the focal task (activation of the focal arm for load-lifting as reflected by the negative wave over the ipsilateral M1 of the postural arm). They supported the 'parallel' mode of coordination between posture and movement suggested by Massion (1992) that the postural and motor commands develop independently and in parallel. In the present study, the MRPs prior to the APA during lateral weight shift and equal-weighted stepping did not differ between the task conditions. In addition, the MMP that might be related to the execution of APA did not differ between lateral weight shift and equal-weighted stepping. The absence of a significant difference in APA-related MRPs between lateral weight shift and equal-weighted stepping suggests that the CNS utilizes the same motor program for the generation of lateral weight shift regardless of whether it precedes stepping or is the focal task. We speculate that the MRPs associated with the APA reflect the postural command in the 'parallel' mode of postural control even though the present results provide no direct evidence of parallel processing of APA and focal task.

Even though the MRPs related to FO were not the primary focus of this study, we observed MRPs prior to FO which were significantly different between equal-weighted stepping and unloaded stepping conditions in both the voltage and frequency domains. While the MRP prior to FO corresponds to the activation of the cortical processes involved in the preparation of FO, the increased negativity in MRP of equal-weighted stepping might be accounted for by the parallel cortical processing required for both the execution of APA (part of the postural command) and preparation of FO. Thus the specific MRPs related to APA and FO in the present study suggest that APAs and focal tasks are organized independently by parallel descending pathways as separate postural and motor commands and are coordinated either subcortically or cortically (Massion, 1992; Viallet et al., 1992; Ng et al., 2013).

In the current study, the duration to peak APA in equal-weighted stepping was significantly shorter than that of lateral weight shift. It has been shown that the duration of APA is reduced when the gait initiation is performed under triggered conditions (auditory cue) than that of self-initiated situations (Delval et al., 2005; Yiou et al., 2012). The shortened duration of time to peak APA in equal-weighted stepping might be due to the subsequent stepping task that the participants need to perform in response to the auditory cue.

ERSPs

The time–frequency analysis demonstrates that a robust mu and phasic beta ERD occurs during the RP related to both the APA and FO followed by mu and beta ERS during the MP and MMP. ERD reflects the state of increased cortical excitability and serves as another indicator of cortical activation apart from the MRPs. Previous EEG studies reported that the RP that starts 2 s prior to the onset of a voluntary self-paced movement was paralleled by mu and beta ERD with similar onset timing and maximum amplitude at Cz for foot movements (Jasper and Penfield, 1949; Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989). This ERD was followed by mu and beta ERS (Neuper and Pfurtscheller, 1996). It was suggested that the involvement of the basal ganglia in motor planning and their projection to the M1 through the thalamus influences the thalamo-cortical rhythmic system which results in mu and beta ERD that precedes a voluntary movement (Pfurtscheller, 1981; Pfurtscheller and Berghold, 1989). However, the beta ERD usually had a phasic character and smaller amplitude compared to that of mu ERD thereby suggesting different functional significances for mu and beta ERD (Jasper and Penfield, 1949; Pfurtscheller, 1981; Pfurtscheller and Berghold, 1989). ERS was interpreted as a correlate of activated neural structures and reflects the sensorimotor integration prior to and during the activation of pyramidal neurons in the M1 (Pfurtscheller et al., 1993; Neuper and Pfurtscheller, 1996). Apart from the mu and beta ERD, a concurrent gamma ERS (30–40 Hz) close to the primary sensorimotor areas was also reported during externally triggered finger, toe, and tongue movements (Pfurtscheller et al., 1993). The gamma ERS reflects the neural interactions between sensorimotor areas during motor programing (Pfurtscheller et al., 1993). Electrocorticographic and stereo-EEG studies in epileptic patients also reported mu and beta ERD in the 5–40 Hz frequency range during RP associated with self-paced finger movements over SMA proper, M1, and primary sensorimotor areas with earliest ERD observed over SMA proper. This ERD was followed by mu and beta ERS in all the three areas (Ohara et al., 2000; Szurhaj et al., 2003). In the present results, the ERD and ERS during the MRP related to APA and FO might reflect the frequency counterpart of the MRPs.

Moreover, mu and beta ERD were reported to be associated with APA during BMLL tasks. Mu ERD related to APA during a BMLL task was observed in healthy adults and children over the postural M1 hand area that corresponds to the postural forearm stabilization (Martineau et al., 2004; Barlaam et al., 2011). In addition, MEG studies showed pre-movement beta ERD associated with APA during BMLL task over the SMA and postural M1 which began approximately 4 s prior to the movement onset (Ng et al., 2011, 2013). The authors suggested that the beta ERD corresponds to the control of APA. The ERSP results in the present study are also in line with these previous results suggesting the role of cortex in generating postural and motor commands in a stepping task.

Movement-related ICs

The ICs that mainly contributed to the MRPs showed a mid-line fronto-central source identification with maximum activation at FCz and Cz. FCz and Cz

electrodes are located above SMA and primary motor foot area (Deecke and Kornhuber, 1978; Pfurtscheller and Berghold, 1989). An extensive body of literature has reported the role of SMA and M1 in voluntary and externally triggered movements. It has been proposed that the SMA proper and M1 is involved in programing, preparation, and execution of voluntary and externally triggered movements whereas the pre-SMA is involved in internal selection of movement (decision making) (Roland et al., 1980; Thaler et al., 1988; Deiber et al., 1991, 1996, 1999; Humberstone et al., 1997; Cunnington et al., 2002). Both pre-SMA and SMA proper receive input from distinct regions within the dentate nucleus of the cerebellum and internal segment of the globus pallidus. SMA proper and M1 have direct corticospinal projections and, as a consequence, both of them can independently generate and control movements (Dum and Strick, 1991; Picard and Strick, 1996; Akkal et al., 2007). Intracranial recordings using subdural electrodes have shown the generation of MRPs that occur prior to the foot movements (RPs and MPs) from contralateral primary motor foot area and bilateral SMA (Ikeda et al., 1992). fMRI studies of motor imagery and observation of gait initiation and stepping reported activations in dorsal premotor cortex, SMA, and dorsal prefrontal cortex (Malouin et al., 2003; Iseki et al., 2008). In addition, there were significant activations in SMA and M1 in a study that compared real locomotion imaged using PET and imagined locomotion imaged using fMRI. In both experiments, the task included gait initiation (la Fougère et al., 2010). Impaired APAs during voluntary upper limb movements were found in patients with SMA lesions (Gurfinkel and Elner, 1988; Viallet et al., 1992). Also, impaired APAs associated with self-initiated stepping were found in PD patients. The APAs were significantly improved with Levodopa medication in these patients (Burleigh-Jacobs et al., 1997). Since one of the major outputs of the basal ganglia is to SMA, the impaired APAs seen in PD patients might be evidence of SMA involvement in APA. The role of SMA in generating APA during stepping was examined by disrupting SMA using repetitive transcranial magnetic stimulation. The authors found decreased duration of APA and proposed that SMA is involved in the timing of APA (Jacobs et al., 2009). Impaired APAs during stepping were also found in patients with stroke who had lesions in premotor cortex (Chang et al., 2010). Single-neuron recording in standing cats during APA prior to the onset of a reach revealed the role of M1 in the generation of APA (Yakovenko and Drew, 2009). The role of M1 in postural control was further explored using single-neuron recordings during posture and reaching tasks in macaque monkeys suggesting specialized control processes for posture and movement (Kurtzer et al., 2005). Based on all these findings, it is possible that the ICs that contribute to the MRPs in our study might represent activations in SMA, premotor cortex, and M1.

CONCLUSIONS

In summary, the current study reveals cortical activations associated with the preparation of the automatic APA that occurs prior to stepping. Comparable preparatory activation was also observed prior to voluntary lateral weight shift and the APA phase of equal-weighted lateral stepping. These findings reinforce the important role of the cortex in anticipatory balance control and also reveal parallels in cortical activation regardless of the context of control (postural component vs. focal component). In addition, we speculate that the specific MRPs related to the APA and focal task appear to indirectly support the 'parallel mode' of control of posture and movement (Massion, 1992). This study enhances our understanding of the role of the cortex in the generation and execution of APA during lower limb movements.

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