Neuroscience 313 (2016) 99–109

CORTICAL CONTROL OF ANTICIPATORY POSTURAL ADJUSTMENTS PRIOR TO STEPPING

J. P. VARGHESE,[a] D. M. MERINO,[a] K. B. BEYER[a] AND W. E. MCILROY[a,b*]

[a] Department of Kinesiology, University of Waterloo, Waterloo, Ontario, Canada

[b] Canadian Partnership for Stroke Recovery, Sunnybrook Research Institute, Toronto, Ontario, Canada

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)

*Correspondence to: W. E. McIlroy, Department of Kinesiology, University of Waterloo, 200 University Avenue, Waterloo, Ontario N2L 3G1, Canada.
E-mail address: wmcilroy@uwaterloo.ca (W. E. McIlroy).
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.

http://dx.doi.org/10.1016/j.neuroscience.2015.11.032
0306-4522/

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