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PERTURBATION-EVOKED CORTICAL ACTIVITY REFLECTS BOTH THE CONTEXT AND CONSEQUENCE OF POSTURAL INSTABILITY

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Abstract—The cerebral cortex may play a role in the control of compensatory balance reactions by optimizing these responses to suit the task conditions and/or to stimulus (i.e. perturbation) characteristics. These possible contributions appear to be reflected by pre-perturbation and post-perturbation cortical activity. While studies have explored the characteristics and possible meaning of these different events (pre- vs. post-) there is little insight into the possible association between them. The purpose of this study was to explore whether pre- and post-perturbation cortical events are associated or whether they reflect different control processes linked to the control of balance. Twelve participants were presented temporally-predictable postural perturbations under four test conditions. The Block/Random tasks were designed to assess modifiability in CNS gain prior to instability, while the Unconstrained/Constrained tasks assessed responsiveness to the magnitude of instability. Perturbations were evoked by releasing a cable which held the participant in a forward lean position. The magnitude of pre-perturbation cortical activity scaled to perturbation amplitude when the magnitude of the perturbation was predictable [$F(3,11)=2.906$, $P<0.05$]. The amplitude of pre-perturbation cortical activity was large when the size of the forthcoming perturbation was unknown (13.8±7.9, 11.4±9.9, 16.9±9.3, and 16.1±10.6 μV for the Block Unconstrained and Constrained and Random Unconstrained and Constrained, respectively). In addition, N1 amplitude scaled to perturbation amplitude regardless of whether the size of the forthcoming perturbation was known (30.1±17.7, 11.4±7.1, 30.9±18.4, 12.4±6.1 μV). This is the first work to examine modifiability in the pre-perturbation cortical activity related to postural set alterations. The cerebral cortex differentially processes independent components prior to and following postural instability to generate compensatory responses linked to the conditions under which instability is experienced.

Key words: evoked potentials, postural set, balance, human.

Compensatory balance responses are essential contributors to one's capacity to prevent falling in the face of postural instability. These responses are generated at short latencies following the onset of instability and scale to the magnitude of instability. Under conditions where the onset or magnitude of instability is unpredictable (such as tripping), the compensatory responses are strongly influenced by the stimulus (Nashner, 1977; Nashner and Cordo, 1981). However, when the characteristics of instability are known (such as self-generated movements or anticipated perturbations), the characteristics of the compensatory responses are modifiable to suit task conditions (Horak et al., 1989). Such modifiability is attributable to alterations in postural set or "state" of the central nervous system (CNS) which occurs in advance of instability and corresponds to expected task conditions (Horak et al., 1989). These alterations occur as a result of past experience or current context; their functional importance in balance control is to optimize the efficiency of compensatory balance responses.

When one considers the factors that contribute to the ability to regulate the gain of the CNS to the expected level of instability, two key factors emerge. The first is the context or the conditions under which the bout of instability is expected to occur. Context is an integral component in set adjustments as internal and external cues provide key information regarding environmental conditions which allows an organism to pre-select the appropriate balance-correcting response (Jacobs and Horak, 2007). The second factor is the consequence or the outcome of instability which is related, in part, to the magnitude of the perturbation. The actual size of instability serves as feedback, allowing for a comparison to be made between a steady state system and a system challenged by instability. Such a comparison provides the CNS with important information for potential future events that may continue to challenge stability. The purpose of the present work is to advance understanding of the association between the pre-perturbation (context-related) and the post-perturbation (consequence-related) cortical activity. Pre-perturbation cortical activity has been suggested to yield insight into the postural set linked to the context of task conditions. However, inferences about postural set have typically come from the examination of the spatiotemporal characteristics of postural responses. These studies have quantified variations

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Abbreviations: ANOVA, analysis of variance; AP, antero-posterior; CNS, central nervous system; COP, centre of pressure; EEG, electroencephalography; EMG, electromyography; EOG, electrooculogram; iEMG, integrated EMG; MG, medial gastrocnemius; TA, tibialis anterior.

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in the timing and magnitude of electromyography (EMG) activity in advance of postural instability by varying either the magnitude (in terms of both velocity and amplitude) or direction of instability (Diener et al., 1988; Horak and Diener, 1994). Yet, despite burgeoning evidence to suggest that electroencephalographic measures (EEG) may be illustrative of alterations in postural set, set-based modifications in cortical activity have not been examined with the same vigour. Pre-perturbation cortical activity associated with temporal predictability of destabilizing events have been observed (Jacobs et al., 2008; Maeda and Fujiwara, 2007; Mochizuki et al., 2008; Yoshida et al., 2008) and may be reflective of alterations in postural set. In the aforementioned work measuring cortical activity, the only modification requiring set adjustments was in temporal predictability but not in the magnitude of instability.

Evoked cortical responses occurring after postural instability (N1) have been thought to represent error detection or allocation of cortical resources in response to meaningful stimuli (Adkin et al., 2006). These responses scale to the magnitude of instability (Camilleri et al., 2006; Staines et al., 2001) and are consistently evoked at a fixed latency following the onset of instability (Mochizuki et al., 2009; Quant et al., 2004b). The spatio-temporal profile of these events depicts a system that is sensitive to the size of the error experienced by the system. As noted, N1 has been linked to a cortical marker for error detection, thus the comparison between expected and actual events and the resulting error that occurs may be an important component for evaluating the extent to which measurable cortical events denote processing linked to postural set.

To date, examinations into the contributions of the cortex to balance control have evolved with pre- and post-perturbation cortical events being explored independently. However, given the tight spatial and temporal coupling between events, it is possible that a functionally meaningful relationship exists between the slow-wave shifts that occur prior to perturbation onset and the multi-phasic potentials evoked after the onset of instability. One can envisage a situation in which the detection of the "error" or mobilization of cortical resources in response to a stimulus could be influenced by the underlying level of the CNS at the time at which the error occurred. In contrast, it is possible that pre-perturbation (context) and post-perturbation (consequence) events reflect entirely independent processes. Under such conditions, pre-perturbation cortical activity may be sensitive to the underlying physiological state, where the magnitude of such activity ought to modulate according to the expected magnitude of the perturbation. This activity would have no bearing on post-perturbation responses, which would only be sensitive to the magnitude of the perturbation. Clarifying the relationship between measurable cortical phenomena continues to advance our understanding of the cortical contributions to the control of stability. Assigning functional significance to individual components of cortical events may be valuable in understanding stability control processes in those for whom fall risk is elevated.

No studies have explored whether the amplitude of pre-perturbation cortical activity is related to the expected amplitude of the perturbation. Thus, the first objective was to determine whether pre-perturbation cortical activity scaled to the anticipated amplitude of perturbation. The second objective was to determine whether the amplitude of the pre-perturbation cortical activity and the evoked N1 response were associated. We asked the question: if the initial pre-perturbation activity was larger, linked to the expectation of a large perturbation, would this influence the amplitude of post-perturbation response? This relationship was explored by manipulating the actual and the anticipated amplitude of applied postural perturbation.

EXPERIMENTAL PROCEDURES

Subjects

Twelve subjects (six male, 29.3±6.4 years, 172.1±9.9 cm, 71.6±15.9 kg) agreed to participate in the study. All subjects were free of neuromuscular disorders and each provided written, informed consent prior to the onset of the study. The study was conducted with approval from the Research Ethics Board at the Toronto Rehabilitation Institute.

Data acquisition

Electroencephalography. Electroencephalographic (EEG) signals were obtained using a 32 channel electrode cap (Quik-Cap, Neuroscan, El Paso, TX, USA) based on the International 10–20 System. The impedance for all channels was maintained below 5 kΩ and all channels were referenced to linked mastoids. The electrooculogram (EOG) was obtained using four electrodes, one superior and one inferior to the left eye, and one just lateral to the left and right eye. Electroencephalographic and EOG signals were sampled at 1000 Hz, filtered (DC-300 Hz) online using a NuAmps amplifier (Neuroscan, El Paso, TX, USA) and stored for offline analysis.

Electromyography. Using self-adhering Ag-AgCl electrodes (Meditrace 130; Kendall, Mansfield, MA, USA) with an inter-electrode distance of 20 mm, surface EMG signals were obtained bilaterally from the medial gastrocnemius (MG), tibialis anterior (TA), and upper fibres of the trapezius muscle using a band-pass setting of 10–300 Hz, amplification×2000 and a sampling rate of 1000 Hz (Noraxon, Scottsdale, AZ, USA). Prior to placement of the electrodes, the skin was abraded and cleaned. A single electrode placed on the anterior aspect of the shin just proximal to the ankle joint on the stance leg (see Electromyography in Data Analysis section) served as a ground.

Centre of pressure and pre-perturbation lean force. Centre of pressure (COP) position was monitored prior to and following the perturbation while subjects stood on two adjacent force plates (50 cm long, 25 cm wide; Advanced Mechanical Technology Inc., Watertown, MA, USA) embedded within a raised platform. A third force plate (51 cm long, 46 cm wide, Advanced Mechanical Technology Inc., Watertown, MA, USA) was positioned in front of the subject to capture footfall on trials requiring a stepping response. Centre of pressure position data were sampled at 1000 Hz and collected for 3 s prior to and 2 s after the perturbation. A cable connecting the participant to the platform (Fig. 1) was affixed to an in-line load cell (Transducer Techniques, Temecula, CA, USA), allowing for quantification of the load exerted on the cable resulting from the participant's lean angle prior to perturbation onset. The sharp drop in cable load observed at the time of the perturbation served as the indicator of perturbation onset time. Load cell data was sampled at 1000 Hz and stored for offline analysis.