PLEASE NOTE: **This is an invited peer-reviewed manuscript for the special issue of the Journal of Neural Transmission related to the conference on Gait and Mental Function** (held in Madrid in February/2006 and organized by Dr. Nir Giladi; nirg@tasmc.health.gov.il)

Title: Cognitive demands and cortical control of human balance-recovery reactions (REVISED April, 2007)

Authors: Brian E. Maki[a,b,c] and William E. McIlroy[a,b,c,d]

Affiliations:
[a]Sunnybrook Health Sciences Centre (Toronto, Canada)
[b]University of Toronto (Toronto, Canada)
[c]Toronto Rehabilitation Institute (Toronto, Canada)
[d]University of Waterloo (Waterloo, Canada)

Correspondence:
Brian E. Maki, PhD, PEng
Centre for Studies in Aging, Sunnybrook Health Sciences Centre,
2075 Bayview Avenue, Toronto, Ontario, CANADA M4N 3M5
Tel: (416) 480-6100 ext. 3513; Fax: (416) 480-5856
E-mail: brian.maki@sri.utoronto.ca

Keywords: attentional dynamics, automatic postural response, dual-task interference, electroencephalography, evoked potentials, eye movements, gaze, grasping, postural balance, reaching, saccades, stepping, transcranial magnetic stimulation, triggered reactions, visual attention

Running head: Cortical control of balance reactions

SUMMARY

A traditional view has been that balance control occurs at a very automatic level, primarily involving the spinal cord and brainstem; however, there is growing evidence that the cerebral cortex and cognitive processing are involved in controlling specific aspects of balance. The purpose of this review is to summarize recent literature pertaining to the cognitive demands and cortical control of balance-recovery reactions, focussing on five emerging sources of evidence: 1) dual-task studies demonstrating that concurrent performance of cognitive and balance-recovery tasks leads to interference effects; 2) dual-task studies that have examined the temporal dynamics associated with the reallocation of cognitive resources to the balance-recovery task; 3) visual attention studies that have inferred contributions of visual attention based on gaze measurements and/or manipulations to occlude vision; 4) measurements of brain potentials evoked by postural perturbation; and 5) use of transcranial magnetic stimulation to alter contributions from specific cortical areas.

Word count = 148 (maximum allowed = 150)

LIST OF ABBREVIATIONS

APA	anticipatory postural adjustment
APR	automatic postural response
CNS	central nervous system
COP	center of foot pressure
EEG	electroencephalography
EMG	electromyography
rTMS	repetitive transcranial magnetic stimulation
TMS	transcranial magnetic stimulation

1. INTRODUCTION

A traditional view has been that balance control occurs at a very "automatic" level, primarily involving polysynaptic pathways within the spinal cord and brainstem (for reviews, see Dietz, (1992) and Horak and MacPherson, (1996)). However, there is more and more evidence that the cerebral cortex and high-level “cognitive” processing may be involved in controlling specific aspects of balance. Although the majority of such studies have looked at the regulation of balance during unperturbed stance and gait (see review by Woollacott and Shumway-Cook (2002)), a small but growing number of studies have begun to examine the cognitive demands of executing the rapid stabilizing reactions that are evoked by postural perturbation and the cortical contributions to the control of these reactions.

Despite a very rapid latency (as early as 80ms after perturbation onset), these balance-recovery reactions are remarkably complex. Triggered and modulated by multiple sensory inputs (somatosensory, vestibular, visual), these reactions are highly adaptable to meet functional demands, as defined by: 1) the features of the perturbation (e.g. timing, direction, magnitude, predictability); 2) the “central set” of the individual (e.g. affect, arousal, attention, expectations, prior experience); 3) ongoing cognitive or motor activity; and 4) environmental constraints on reaction-force generation and limb movement (Maki, 2007). The historical view of balance reactions, involving stereotyped spinal reflexes, would not appear to be consistent with this level of complexity and modifiability.

The purpose of this review is to summarize recent literature pertaining to the cognitive demands and cortical control of these balance-recovery reactions in humans. For the purposes of this review, we define a “cognitive” task to be any task that involves attention, perception, memory, decision-making and/or volitional motor action. Indirect evidence for cognitive demands and cortical control can potentially be inferred from a wide range of sources, e.g. effects of experimentally-induced lesions or electrical stimulation in animal preparations (Horak and MacPherson, 1996; Macpherson et al, 1997), clinical or epidemiological studies of instability or falls in persons with cognitive disorders (Alexander et al, 1995), and studies demonstrating the capacity of the central nervous system (CNS) to adapt to predictable features of the perturbation or task conditions (Horak, 1995).

This review, however, will focus on five relatively new sources of evidence that currently appear to be emerging (or re-emerging) in the literature: 1) dual-task studies that have demonstrated that concurrent performance of cognitive and balance-recovery tasks leads to interference effects, i.e. impaired performance of one or both tasks; 2) dual-task studies that have examined the temporal dynamics associated with the allocation or switching of cognitive resources to the task of balance recovery; 3) visual-attention studies that have inferred contributions of visual attention and visuospatial processing on the basis of gaze measurements and/or manipulations to occlude vision during specific phases of the balance reactions; 4) measurements of brain potentials that are evoked by postural perturbation; and 5) use of transcranial magnetic stimulation (TMS) to alter the contributions from specific cortical areas during perturbation-evoked balance reactions.

Although some researchers have begun to examine the influence of cognitive impairment (e.g. Alzheimer's disease) on reactive balance control (Chong et al, 1999), the vast majority of studies to date have involved healthy young (e.g. 20-40yrs) and older (e.g. 65-80yrs) adults having no documented cognitive impairments; hence, we will restrict the focus of this review to these studies. The majority of the studies that will be reviewed have examined reactions to perturbation of standing balance, and this can be assumed to be the case unless specified otherwise. These reactions are most commonly evoked via sudden motion (translation or rotation) of a platform on which the subject stands.

An important point that will emerge from this review is that the cognitive demands and cortical contributions vary depending on the balance-recovery strategy that is selected, as well as the phase of the reaction (within the selected strategy). Balance-recovery reactions involve two distinct classes of strategies: 1) change-in-support strategies, which involve very rapid movement of the limbs (stepping, or reaching to grasp or touch an object for support) so as to alter the base of support, and 2) fixed-support (feet-in-place) strategies, which involve rapid generation of stabilizing joint torques that act to keep the body's center of mass within the limits of the existing base of support (Maki and McIlroy, 1997; Maki and McIlroy, 2005) (Figure 1). The early fixed-support reaction to antero-posterior perturbation involves activation of the ankle muscles at a latency of approximately 80-140ms (Figure 1a), and is commonly known as the "automatic postural response" (APR) (Nashner and McCollum, 1985). The APR acts to arrest the initial falling motion of the body, and appears to be a triggered reaction (typically, ~100ms in duration) involving preprogrammed muscle synergies that are scaled according to the perturbation-evoked sensory drive, as well as the functional demands dictated by the situation and environment. The subsequent phase(s) of the reaction act to restore the body to an upright equilibrium posture. The defining features of these later phases are less clearly prescribed than the APR but likely involve ongoing feedback control.

The APR also occurs during change-in-support reactions (Figures 1b, 1c). Typically, stepping reactions are preceded by the APR, whereas reaching reactions can occur in parallel with the APR (Maki and McIlroy, 1997). Forward and backward stepping reactions may also involve a so-called "anticipatory postural adjustment" (APA) that precedes the swing and landing phases. The APA phase serves to propel the center of mass laterally toward the stance leg prior to foot-lift and thereby helps to counter the tendency of the body to fall toward the unsupported side during the swing phase. Such APAs occur invariably during volitional step initiation but are often absent or severely truncated during perturbation-evoked stepping reactions (McIlroy and Maki, 1993). The omission of the APA (typically, 100-150ms in duration) allows a more rapid response but leads to lateral instability, requiring the lateral center-of-mass motion that occurs during the swing phase to be arrested during the landing phase (McIlroy and Maki, 1999). Large APAs can, however, occur when lateral stability is severely challenged by the task conditions, e.g. when a prolonged swing duration is required in order to direct the perturbation-evoked step over an obstacle (Zettel et al, 2002).

In comparing studies, it is important to note that support-surface perturbations actually comprise two distinct perturbations, associated with the platform acceleration and the platform deceleration. While the APR is evoked by the platform acceleration, the platform deceleration can evoke a response in the APR antagonists (McIlroy and Maki, 1994). It appears that this "deceleration response" is most likely to occur if the perturbation is relatively long in duration (e.g. >500ms). In other respects, however, the fixed-support and change-in-support reactions evoked by different perturbation types and durations (typically ranging from 100 to 600ms) appear to involve quite similar sequencing and timing of phases.

2. DUAL-TASK INTERFERENCE

Much of the evidence for cortical/cognitive contributions to balance control comes from dual-task studies. Typically, these studies show that simultaneous performance of a balance task interferes with performance of the concurrent cognitive task, although reciprocal effects on the performance of the balance task can also occur. Since the simultaneous balance task impairs performance of the cognitive task, it is inferred that the balance task demands attention or other cognitive resources. Dual-task interference effects have been demonstrated using a wide range of different cognitive tasks (e.g. mental arithmetic, spatial memory, visual perception, reaction time, inhibitory reactions, sentence completion, visuomotor tracking). However, relatively few studies have involved balance tasks that entail reacting to a sudden perturbation, focussing instead on regulation of balance during quiet stance, steady-state gait or obstacle avoidance (Woollacott and Shumway-Cook, 2002).

A number of theories have been proposed to explain dual-task interference effects (Pashler, 1999). According to capacity theories, task performance suffers because both tasks have to compete for, or somehow share, a finite pool of cognitive resources. Bottle-neck theories propose that performance suffers because both tasks have to queue up to use a single critical information-processing channel. Cross-talk theories propose that the processing of one task in effect creates noise that interferes with performance of the second task. Finally, neural-structure theories propose that dual-task interference effects occur because there are competing demands for specific neural pathways within the brain.

A small but growing number of dual-task studies have provided evidence that execution of balance-recovery reactions does require cognitive resources. For example, in a study by Brown et al (1999), platform perturbations were administered while young and older adults performed a mental arithmetic task (counting backward by serial 3's). Results showed that there was a delay between counting responses during the reaction to the perturbation, compared to the counting performed prior to perturbation onset. Interestingly, use of a stepping reaction to recover balance appeared to place greater demands on cognitive resources in the older adults, as evidenced by a more pronounced slowing in the counting task, compared to trials where they did not step (Figure 2a). Performing the cognitive task also had some reciprocal effects on the balance-task performance, but these effects were relatively small and occurred primarily during the later phases of the postural reaction. For example, in the fixed-support balance reactions (no stepping), the counting task caused a significant reduction (by ~25%) in activation of gastrocnemius (one of the main ankle agonists) over a time interval of 350-500ms after perturbation onset, but did not affect activation of this muscle during earlier time windows (Rankin et al, 2000).

Similarly, Norrie et al (2002) examined fixed-support balance reactions evoked by small platform translations and found that their cognitive task (visuomotor pursuit tracking of a target on a computer screen; see Figure 4) led to modest changes in the later phases (>250ms after perturbation onset) of the balance reactions (e.g. 5-14% increase in peak excursion of the center of foot pressure, COP), but did not affect the COP displacement or ankle electromyographic (EMG) activity associated with the earliest phase of the reaction (i.e. the APR). This also agrees with the results of Redfern et al (2002), who found that performance of a concurrent volitional reaction-time task did not affect the latency or amplitude of the initial peak in COP displacement (which typically occurred within ~300ms after perturbation onset) evoked by small platform translations. These results are consistent with the view that compensatory balance reactions, even those evoked by small perturbations, are characterized by distinct phases distinguished in part by an initial "automatic" phase (i.e. the APR) and one or more later phases exhibiting an increased reliance on cognitive resources (McIlroy et al, 1999; Norrie et al, 2002). An alternate interpretation, proposed by Redfern et al (2002), is that the APR does require cognitive resources, but is not affected by the cognitive task because the CNS assigns top priority to the task of postural stabilization and immediately allocates all of the cognitive resources needed to execute the balance reaction effectively.

Brauer et al (2002) used a concurrent auditory reaction-time task to study the cognitive demands of compensatory stepping reactions evoked by platform translation. Subjects had to react to the auditory stimulus by speaking a word. During each trial, a series of ten auditory stimuli was presented and the perturbation onset was triggered to occur unpredictably at the same time as one of these stimuli. Although execution of the stepping reaction caused a delay in auditory reaction time in both young and older adults, the most pronounced delay occurred in a group of balance-impaired older adults (Figure 2b). Essentially, these subjects delayed their response to the auditory cue until after the stepping reaction was completed. Similar to the results noted above, use of a stepping reaction led to greater slowing of reaction time and hence appeared to place greater demands on cognitive resources in comparison to fixed-support reactions, but performing the cognitive task had little or no effect on the characteristics of the stepping reactions.

Using the visuomotor-tracking paradigm (Figure 4), Zettel et al (2007) found that performance of this cognitive task also had little influence on the characteristics of perturbation-evoked stepping reactions in healthy young adults, even when challenging environmental constraints (i.e. the obstacles and/or step targets depicted in Figure 5a) increased the demands for accurate foot movement. In older adults, however, the duration and amplitude of the "anticipatory postural adjustment" (APA) that preceded foot-lift in the obstacle trials were each reduced (by ~30%) when performing the tracking task. This resulted in a 67% increase in lateral center-of-mass displacement during step execution. The control of these APA's is believed to involve cortical processing (e.g. supplementary motor area) (Massion, 1991). Potentially, an impaired ability of older adults to rapidly and effectively reallocate cortical resources from the tracking task to the balance-recovery task (see Section 3) may have led to the compromised anticipatory control of lateral stability during the stepping reactions. Presumably, the younger adults were able to avoid this problem because they had the ability to switch attention quickly enough to dedicate sufficient cognitive resources to the "anticipatory control" phase of the stepping reaction.

The results from these various dual-task studies provide clear evidence that the balance-recovery task does create a demand for cognitive resources and that more complex balance reactions such as stepping can create a greater demand compared to fixed-support reactions, particularly so in older adults. However, these studies provide little or no information about the "attentional dynamics", i.e. the temporal features of the processing. For example, does the processing for the two tasks occur in parallel, with sharing of resources, or is there a sequential control, with a distinct switching of attention and reallocation of other cognitive resources between tasks? If so, does aging affect ability to reallocate cognitive resources rapidly and effectively?

3. ATTENTIONAL DYNAMICS

One approach that has been used to examine the attentional dynamics involves a variation of the dual-task paradigm wherein the interval between a volitional reaction-time stimulus and the onset of the postural perturbation (the “stimulus onset asynchrony”) is tightly controlled. Redfern and colleagues (2002) have used this approach, presenting a visual or auditory reaction-time probe at a number of time points in relation to the platform perturbation. They found that volitional reaction time was slower when the stimulus was delivered either at the same time as perturbation onset or 100ms later, compared to when the stimulus was delivered 250ms or more after perturbation onset (Figure 3). Based on this study and a similar but later study (Muller et al, 2004), these authors concluded that the cognitive demands of planning and executing the postural reaction were limited to a very brief interval during the initiation of the postural reaction, and suggested that the delay in the voluntary reaction-time response during this interval was the result of a processing bottle-neck related to response-selection mechanisms (Muller et al, 2004). Their initial study also demonstrated that there was a delay in responding to the reaction-time stimulus when it was delivered 100ms prior to perturbation onset, suggesting possible dual-task interference with processing related to preparation for the forthcoming postural perturbation.

McIlroy, Maki and colleagues developed a different type of dual-task paradigm to study attentional dynamics during balance reactions, and have used this paradigm in a number of studies (McIlroy et al, 1999; Maki et al, 2001a; Maki et al, 2001b; Norrie et al, 2002; Zettel et al, 2005a; Zettel et al, 2006). This paradigm is designed to estimate the specific point in time at which cognitive resources are switched from an ongoing cognitive task to the balance-recovery task. This cannot be accomplished using cognitive tasks that require responses at discrete points in time, because attention can be switched during the intervals before or after each discrete cognitive-task response. In order to monitor switching of attention, it is necessary to use a cognitive task that requires continuous performance. These authors used the continuous visuomotor tracking task mentioned earlier, in which subjects use one hand to control a cursor to track a target that moves continuously but unpredictably on a computer screen (Figure 4). In studies involving large perturbations, the hand and tracking device are immobilized with respect to each other by means of a splint, sling and restraining straps. This prevents the perturbation from causing mechanical disruption of tracking performance and also typically inhibits postural arm reactions (as confirmed by monitoring of EMG) that could potentially interfere with the tracking. The balance perturbation is applied as the subject performs the tracking task, and typically leads to a sudden deviation in tracking (either a complete pause in tracking or a statistically significant increase in tracking error) that begins approximately 200-400ms after perturbation onset (Figure 4c). The start of the tracking deviation is inferred to mark the instant at which attention and other cognitive resources were switched to the task of recovering balance.

The initial tracking studies involved a simulated balancing task that required subjects to generate ankle torque on a foot pedal so as to keep an inverted-pendulum load upright during a sudden perturbation to the pendulum (McIlroy et al, 1999). Subsequent tracking studies involved the use of small platform-translation perturbations to evoke feet-in-place reactions in standing subjects (Maki et al, 2001b; Norrie et al, 2002). The results were very similar in both types of studies. A key observation was that the switching of attention (as inferred from onset of tracking deviation) typically began 100-300ms after the earliest postural reaction in the ankle muscles. As noted earlier, this ankle reaction has been termed the “automatic postural response” (APR), and these results support the view that the earliest reaction is, in fact, largely “automatic”. Conversely, the tracking deviation almost always occurred well before the peak in the stabilizing response (as indicated by the COP displacement, which typically peaks ~400-500ms after perturbation onset), suggesting that the attention switching may have played a role in controlling the peak response, as well as subsequent efforts to return the body to an upright equilibrium position. Results also showed that attention switching was delayed (by 130ms, on average) in older adults, and that this delay correlated with a delay in generating the peak stabilizing COP response (Maki et al, 2001b). The latter finding raises the possibility that slowing of attentional dynamics may actually be an important factor that contributes to age-related deterioration in balance control. In other words, a delay in switching attention and other cognitive resources to the balance-recovery task may underlie impaired planning and/or execution of specific aspects of the balance reaction that are dependent on those resources.

The results from these tracking studies contrast sharply with the results from the reaction-time studies of Redfern et al (Redfern et al, 2002; Muller et al, 2004), who found that it is the earliest phase of the postural reaction that requires cognitive resources. The discrepancy could be due to a number of factors, including differences in the attention-switching requirements (disengaging from an ongoing cognitive task versus initiating a response to a stimulus) and cognitive-task complexity (visuomotor tracking versus simple reaction time). In addition, the use of much briefer perturbations by Redfern et al (250ms versus 600ms) may have limited opportunity to delineate later phases of the response (such as the response associated with the onset of platform deceleration).

Another series of tracking studies involved use of larger platform perturbations to evoke compensatory stepping reactions (Maki et al, 2001a; Zettel et al, 2005a; Zettel et al, 2006). Some of these studies included task conditions in which constraints on foot movement (i.e. the obstacles and/or step targets depicted in Figure 5a) increased the demands for accurate control of the step trajectory (Zettel et al, 2005a; Zettel et al, 2006). As in the previous tracking studies, the onset of tracking error occurred after the earliest postural EMG activity evoked at the ankle. The tracking deviation typically began very close to onset of the stepping reaction (as marked by the divergence in the left and right vertical ground-reaction forces; see Figure 1b) and almost always occurred prior to foot-off. These findings suggest that it may be the planning of the foot lift and/or foot trajectory that normally requires cognitive resources. This is further supported by findings that attention switching (in young adults) occurred most frequently in the trials that demanded the most accurate control of the foot movement (99% of trials that involved both a step target and an obstacle) and least frequently in trials where there were no constraints on foot trajectory (81% of these trials).

As in the previous studies of feet-in-place reactions, the onset of tracking error in the stepping studies was significantly delayed (by ~30ms, on average) in older adults (Zettel et al, 2006). In addition, in contrast to the young adults, older subjects showed a near-equal tendency to switch attention across all constraint conditions (>93% of trials in each condition). The higher incidence of attention switching in the less demanding tasks, in comparison to the young subjects, suggests that older adults either assigned higher priority to the balance-recovery task (Shumway-Cook et al, 1997) or were more dependent than the young on using high-level processing to control the stepping reactions. Additional involvement of high-level processing and recruitment of cortical areas during motor tasks is thought to be one mechanism by which the CNS attempts to compensate for age-related neural degeneration (Ward and Franckowiak, 2003).

In summary, it does appear that the CNS is normally able to rapidly switch attention and other cognitive resources from an ongoing cognitive task to the task of balance recovery, when required. This switching appears to occur after the earliest phase of the postural reaction (i.e. the APR) and typically occurs prior to the onset of stepping movements; however, older adult exhibit a delay in attention switching, which appears to compromise specific aspects of the balance-recovery reaction. In the absence of an ongoing cognitive task, it appears that cognitive resources can be allocated to the balance-recovery task in an anticipatory manner, prior to perturbation onset, and that these resources remain allocated to this task during the earliest phase of the reaction. Presumably, however, this anticipatory allocation of cognitive resources requires prior expectation that a perturbation is forthcoming, and hence is unlikely to be an effective strategy in the conditions of daily life, where perturbations tend to arise unexpectedly. One key aspect of postural behavior that is absent from the studies reviewed in this section involves the need to modulate the postural reaction in order to accommodate environmental constraints on limb movement and to allocate visual attention in order to acquire the requisite visuospatial information. Recent balance-perturbation studies have begun to evaluate these cognitive demands by manipulating visual inputs and by measuring gaze behavior.

4. VISUAL ATTENTION AND GAZE BEHAVIOR

Visual attention and associated gaze behavior have yet to receive much attention in the context of balance-recovery reactions. However, it is clear that visuospatial information about the environment is often required to execute balance-recovery reactions successfully, particularly when the reactions involve rapid limb movements such as stepping or reaching (Maki et al, 2003; Maki and McIlroy, 2005). Stepping reactions must be controlled to avoid obstacles and other constraints on foot movement, while reaching reactions must be directed toward some object that can be touched or grasped for support.

Although the visual control of volitional limb movement has been studied quite extensively, the findings may not necessarily apply to the control of the much more rapid movements that are triggered by postural perturbation. In contrast to volitional movement, reactions evoked by sudden unpredictable balance perturbation cannot be planned in advance, as the limb movement must be modulated to accommodate and arrest the perturbation-induced falling motion. In addition, the urgent need to react rapidly may severely limit the opportunity for “online” acquisition of salient visuospatial information about the surroundings (Maki et al, 2003; Maki and McIlroy, 2005). It has been proposed, instead, that an egocentric spatial map is formed and updated automatically as persons move about in their daily lives, as a contingency, to allow the foot or hand to be moved very rapidly in an appropriate direction if and when a sudden loss of balance does occur (Ghafouri et al, 2004; Zettel et al, 2005a).

To study the role of visual attention in the control of stepping reactions, Zettel et al (2005a; 2005b) used a motion platform to deliver unpredictable multidirectional perturbations while subjects performed the visuomotor tracking task described earlier, and used an eye tracker to monitor changes in gaze direction. To increase demands for accurate control of the foot trajectory, task conditions were included where the subject had to modulate the stepping reaction so as to move the foot over a challenging obstacle and/or land the foot on a target line, in responding to the perturbations that caused the body to fall forward (Figure 5a). Remarkably, both young and older adults were commonly able to do this successfully (cleared obstacle in >75% of trials, landed on target in >40% of trials), and did so without looking down toward the feet or floor in the majority of trials (Figure 5b). These findings suggest that visual attention and working spatial memory may play a critical role, prior to perturbation onset, in acquiring and storing the visuospatial environmental information needed to help guide the foot movement during a subsequent stepping reaction.

A second objective of these studies was to determine if the attention switching that follows perturbation onset (as inferred from onset of significant error in performing the viusomotor tracking task) was related to shifting of gaze direction. It clearly was not. Tracking deviation occurred in more than 90% of trials, whereas gaze shift occurred in less than 17% of trials (Figure 5b, 5c). Furthermore, in the few trials where downward gaze shift did occur, the tracking deviation usually began well before the gaze shift, and there was no consistent temporal relation between the two events. These findings suggest that the attention switching is associated with controlling other aspects of the balance-recovery reaction, unrelated to acquisition of visuospatial environment information.

In a subsequent study, Zettel et al (2005c) examined gaze behavior in a more demanding situation. Subjects stood on a motion platform amid multiple obstacles that were controlled to move intermittently in an unpredictable manner, and the stepping reaction had to be controlled to avoid the obstacles (Figure 6a-c). To prevent learning of predictive control strategies, subjects performed only one trial (their very first exposure to the perturbation and environment). Visual scanning of the obstacles and surroundings occurred prior to perturbation onset in all subjects; however, gaze was never redirected at the obstacles, step foot or landing site in response to the perturbation. Surprisingly, the point of gaze at time of foot contact was consistently and substantially anterior to the step-landing site. Despite the apparent absence of “online” visual feedback related to the foot movement, the compensatory step avoided obstacle contact in 10 of 12 young adults and 9 of 10 older subjects. The results indicate that the balance-recovery reaction was typically modulated on the basis of visuospatial environmental information that was acquired and continually updated prior to perturbation, as opposed to a strategy based on “online” visual control. The older subjects were equally able to avoid obstacle contact despite the fact that they looked downward less frequently than younger adults during the pre-perturbation interval.

A study by Scovil et al (2007) also involved unpredictable obstacles. Subjects stood on a motion platform, behind a barrier that had a narrow slot through which the foot could be moved forward (Figure 6d, 6e). The slot location was varied randomly between trials, and subjects were prevented from seeing the slot location prior to the start of the trial. Liquid crystal goggles were used to occlude vision either prior to or after perturbation onset, thereby forcing reliance on either “online” or “stored” visuospatial information, respectively. When forced to use online visual control, subjects were less able to reliably select the most appropriate foot for stepping, and step modifications appeared to be directed at increasing the amount of time available for visuospatial scanning and processing. This suggests that online visual control does not allow for optimal planning of rapid stepping reactions and may be sufficient only if the step reaction can be delayed.

Ghafouri et al (2004) examined visual control strategies associated with rapid reach-to-grasp reactions evoked by unpredictable lateral platform motion. Subjects were instructed to recover balance by grasping a handrail at a marked location. In some blocks of trials, liquid crystal goggles were used to block vision at time of perturbation onset. Results showed that the initial arm trajectory (first 100ms) and associated muscle activation were heavily modulated to take into account the direction and speed of the perturbation-induced body motion in relation to the handrail. However, this modulation was unaffected by occlusion of vision at perturbation onset, indicating that “stored” visuospatial information about the rail location was incorporated into the control. These findings are consistent with the view that the CNS modulates the initial arm trajectory by combining an egocentric spatial map of the surroundings, formed prior to perturbation onset, with online multisensory feedback about the body motion.

To better understand the role of visual attention in controlling balance reactions in “real-life” situations, Maki and colleagues (Cejka et al, 2005; Lee et al, 2007; Maki et al, 2006; McKay et al, 2007) have developed a protocol to investigate the reaching reactions and associated gaze behavior that occur when responding to a perturbation that is truly unexpected, while ambulating in an unfamiliar environment for the very first time. Subjects were given the task of making a phone call, which required opening a door and walking to the far end of an extended (2x6m) motion platform (Figure 7). The platform was configured to simulate an office environment, including a stair, handrail and various visual distracters, and was triggered to move suddenly as the subject approached the handrail. A deception was used to ensure that the first perturbation was truly unexpected. Preliminary testing has indicated that reactions to grasp the handrail are typically executed successfully without any online visual fixation of the rail or hand (Cejka et al, 2005; Lee et al, 2007). Instead, subjects typically directed one or more saccades toward the rail upon entering the environment, consistent with the use of a preformed spatial map to help guide the reaching reaction. It did appear, however, that online visual control (involving central and/or peripheral fields) may have contributed to correction of errors (e.g. overshoot) during final target acquisition and prehension, in some trials (King et al, 2007; Lee et al, 2007).

In summary, the studies described in this section suggest that the task of monitoring the location and spatial features of nearby environmental constraints is typically performed on an ongoing basis in a proactive manner, i.e. as a contingency in the event that sudden loss of balance occurs. This strategy allows both vision and attention to be allocated to other demands during the execution of the balance-recovery reaction, as detailed in the preceding discussion of dual-task experiments. In initial studies, a tendency of older adults to avoid looking down to monitor their surroundings did not appear to jeopardize successful execution of subsequent stepping reactions; however, more research, involving more demanding task conditions and more complex environments, is needed to determine the full impact of age-related changes in gaze behavior and visual attention. Together, dual-task and gaze-behavior studies provide important evidence about the cognitive demands of planning and executing balance-recovery reactions; however, such studies cannot provide any direct information about the specific cortical loci that are involved or the temporal sequence in which these loci are activated. The approach that has been used most commonly to address these latter issues involves measurement of perturbation-evoked cortical potentials.

5. PERTUBATION-EVOKED BRAIN POTENTIALS

Electroencephalographic (EEG) scalp-electrode recordings of the cortical potentials that are evoked by postural perturbation can provide important temporal information about the cortical processing of the related sensory and motor events. In addition, the distribution of cortical activity across the array of scalp electrodes can provide a gross estimate of the involved loci, and this can be refined to some extent through localization techniques such as Laplacian mapping and dipole source analysis (Wikswo et al, 1993; Gordon and Rzempoluck, 2004). Much of the initial work in this area was performed in the early 1980's; however, there has recently been a resurgence of interest.

Both early and recent studies have consistently shown that unpredictable postural perturbation can elicit a multi-component cortical response that comprises a small positive potential (P1) at a latency of ~40-50ms, followed by a large negative peak (N1) at a latency of ~100-200ms and a second positive potential (P2) that occurs after the N1 response (Dietz et al, 1984; Dietz et al, 1985a; Dietz et al, 1985b; Ackermann et al, 1986; Dimitrov et al, 1996; Duckrow et al, 1999; Quant et al, 2004a; Quant et al, 2004b; Quant et al, 2005) (Figure 8a). Dietz and colleagues (1984; 1985b) suggested that the P1 peak reflects an initial sensory-evoked cortical response. This response varies in amplitude depending on perturbation characteristics, but is relatively small (often less than 1μV) and is not observed consistently (Quant et al, 2004b; Quant et al, 2005).

The evoked negativity (N1) is the most pronounced and consistent feature of the perturbation-evoked cortical response, and has received the most attention in the literature. The N1 peak is large in amplitude (often in excess of 30μV) and is not dependent on the presence of a measurable P1 response (Quant et al, 2005). The N1 emerges, with comparable latency and amplitude characteristics, in a variety of different perturbation and task conditions including: platform perturbation of stance (Dietz et al, 1984; Dietz et al, 1985a; Dietz et al, 1985b; Ackermann et al, 1986; Dimitrov et al, 1996; Duckrow et al, 1999; Quant et al, 2004a; Quant et al, 2005), sternal-nudge perturbation of stance (Adkin et al, 2006), seated whole-body translations with eyes open or eyes closed (Staines et al, 2001), and a seated balancing task that involved use of a foot pedal to keep an inverted-pendulum load upright (Quant et al, 2004b). The topographical distribution of the N1 response suggests an origin in frontocentral cortical regions (Quant et al, 2004b; Adkin et al, 2006) (Figure 8b). This has led to speculation about the possible involvement of the supplementary motor area and/or cingulate cortex; however, more sophisticated localization techniques, such as dipole modelling, will be needed to provide more definitive evidence about the underlying loci.

Dietz et al (1984; 1985b) proposed that the N1 potential reflects cortical processing of afferent input arising from the balance disturbance. Based on effects of ischemic blockade of group Ia afferents and sural nerve stimulation, they concluded that the N1 sensory processing involved proprioceptive and cutaneous inputs from the lower extremities (Dietz et al, 1985a). Consistent with the view that the N1 response is strongly associated with sensory events, the amplitude of the N1 peak is scaled according to the perturbation amplitude (Staines et al, 2001). However, the consistent appearance of a large N1 peak under a wide variety of task conditions, and the modifiability in response to changes in task conditions (as detailed below), suggest that the N1 is more likely to be a generalized response that is independent of the specific sensory modality used to represent the applied perturbation. It is also important to note that there is evidence that the N1 is not specifically associated with motor events. Using the simulated balance task (foot pedal and inverted-pendulum load) described above, Quant et al (2004b) showed that comparable N1 responses occurred whether or not a motor reaction was evoked by the perturbation.

The N1 response has been shown to be modifiable, beyond the perturbation-amplitude dependence already mentioned. For example, Staines et al (2001) found that ongoing sensory discharge, unrelated to the applied perturbation, can attenuate the N1 amplitude. Other studies have shown that the N1 is modulated in response to change in stance width (Dimitrov et al, 1996) and is affected by aging, with older adults showing a 30-50% reduction in N1 amplitude in comparison to young adults (Duckrow et al, 1999). Quant et al (2004a) demonstrated that the N1 response was attenuated during the concurrent performance of the visuomotor tracking task described earlier (mean amplitude of 18μV, versus 27μV in no-tracking trials), suggesting that the N1 may be associated with some of the dual-task interference effects that were noted earlier.

An important observation that influences the interpretation of the N1 response is the effect of stimulus predictability. Dietz et al (1985b) demonstrated that the N1 potential is modifiable according to task conditions, showing that the peak was attenuated when the perturbation was self-initiated; however, it was not clear whether this was a consequence of the increased predictability in perturbation-onset time or other cognitive or psychological factors. A recent study provides compelling evidence that predictability is a key factor, showing that the N1 peak essentially disappeared when perturbation timing was predictable but immediately re-emerged when a “surprise” trial was introduced after a series of predictable trials (Adkin et al, 2006) (Figure 8c). The N1 responses were absent in the predictable trials even though motor responses were evoked. These findings suggest that the N1 potential is not simply related to afferent processing, and may be more closely linked to “event detection”. In this respect, the N1 may have parallels to the "error-related” or “mismatch” negativity that has been reported in other contexts, e.g. responses to novel acoustic stimuli (Schröger, 1996).

The later component of the perturbation-evoked response, often referred to as the P2 potential, is complex and variable. Quant et al (2005) observed that the timing of this potential (~200-400ms after perturbation onset) in platform-perturbation trials coincided approximately with the time at which the platform began to decelerate. This raises the possibility that P2 represents sensory processing related to platform deceleration; however, it could also represent processing of the later phases of the postural response evoked by the initial platform acceleration. To investigate this, these authors compared responses to a perturbation in which the platform deceleration pulse occurred immediately after the acceleration pulse versus a perturbation in which the deceleration pulse was delayed by 500ms (Quant et al, 2005). The deceleration pulse clearly evoked a postural EMG reaction, regardless of the timing of the deceleration; however, the delayed deceleration did not evoke a delayed P2 response. In fact, the P2 timing and amplitude were very similar for both perturbation waveforms, indicating that the P2 potential was not related to the balance response evoked by the platform deceleration. The authors speculated that P2 might instead be related to the reallocation of cognitive resources needed to execute later phases of the postural reaction evoked by the initial platform acceleration. Clearly, however, further work is needed to elucidate the functional role of the P2 potential and the possible link to cognitive events. In particular, it may be useful to compare the perturbation-evoked potentials, and underlying dipoles, to the potentials evoked during non-postural tasks having similar cognitive requirements.

In summary, evoked-potential studies have begun to provide direct electrophysiological evidence about the involvement of cortical centers in the processing of rapid balance-recovery reactions. Although further work is needed to understand the later cortical potentials that can occur, robust evidence of early cortical involvement typically occurs within 100-200ms after perturbation onset (N1 potential), and it appears that this early potential is related to the detection of instability. Interestingly, the N1 is attenuated in older adults. Although the N1 potential appears to be centered over frontocentral cortical regions, balance-perturbation studies have yet to take advantage of available localization techniques (such as Laplacian mapping and dipole source analysis) to provide more precise identification of the involved cortical loci. A complementary approach to identifying these loci involves the use of transcranical magnetic stimulation.

6. TRANSCRANIAL MAGNETIC STIMULATION

Transcranial magnetic stimulation (TMS) is a relatively new technique that offers the potential to explore cortical contributions to balance control by elevating the excitability of specific cortical areas and pathways (Stewart et al, 2001). To date, however, very few studies have applied this technique to balance-recovery reactions. Studies to date have involved stimulation of the motor cortex, but have apparently been limited to fixed-support reactions evoked by relatively small perturbations (Keck et al, 1998; Taube et al, 2006). A methodological challenge, which will be exacerbated in studying responses that involve a greater degree of body motion, pertains to the stabilization of the stimulator coil that is affixed to the head. In the studies reviewed here, subjects wore a rigid halo vest in order to maintain a stable simulation site.

The authors of this review are currently exploring the use of repetitive TMS (rTMS) in which a prolonged period (e.g. 10–30 minutes) of repeated stimuli leads to a sustained change in cortical excitability (Maeda et al, 2000). The effect on the balance-recovery reactions can then be tested after application of the rTMS. This approach negates the need to fixate the coil during the balance testing, and thereby avoids associated problems (e.g. potential effects of the rigid vest and the weight of the coil on the response to the perturbation). While there remain challenges in the interpretation of results and determination of optimal stimulus parameters, the rTMS technique affords the opportunity to use image-guided localization to accurately position and maintain the coil with respect to targeted cortical regions. This is critical when focusing on regions other than primary motor regions, where biomarkers of stimulus integrity, such as motor thresholds, are not available. This is particularly important given the emerging interest, resulting from EEG studies, in the contributions of the frontal association and parietal regions to the control of compensatory balance reactions.

In an early study, Keck et al (1998) applied TMS to the motor cortex during different time-intervals before and during the delivery of a small platform perturbation that evoked an early fixed-support balance reaction at the ankle (tibialis anterior). The influence of corticospinal inputs was assessed by investigating the modulation of tibialis-anterior motor responses evoked by TMS before and during the postural perturbation, and by comparing this to the modulation observed during a voluntary ankle movement. The absence of facilitation in TMS-evoked motor responses measured during the contraction associated with the balance reactions, as compared to facilitation of such TMS-evoked responses during voluntary contractions, led the authors to conclude that the early balance reaction (~80ms latency) was mediated primarily by spinal pathways, rather than the motor cortex.

More recently, Taube et al (2006) performed a TMS study in which they used sub-threshold TMS to condition the H-reflex evoked by peripheral nerve stimulation, in an effort to control for possible effects of the TMS on the excitability of the spinal motoneurons. TMS and nerve stimulation were both adjusted to evoke motor responses in soleus (an ankle extensor agonist) that coincided with different peaks in soleus activation evoked by backward platform translation. When TMS was triggered so that the evoked motor response in soleus coincided with the peaks of the “short-latency” (<60ms) and “medium-latency” (60-85ms) components of the perturbation-evoked reaction, activation of soleus was unaffected. However, the activation was enhanced when the motor response evoked by the TMS coincided with the “long-latency” (>85ms) peak in the balance reaction, and the facilitatory effect of sub-threshold TMS on the H-reflex was also limited to the “long-latency” response. The authors interpreted these findings as indicating that increased cortical excitability led to the augmentation of the response, and concluded that the response in soleus occurring after ~85ms was at least partly mediated by the motor cortex and direct corticospinal pathways. It should be noted that this component of the response likely corresponds to the “automatic postural response” (APR) described earlier in this review.

The potential role of the motor cortex in controlling balance reactions, as suggested by Taube et al (2006), is also supported indirectly by TMS studies of unperturbed stance, which have demonstrated that the motor cortex is capable of exerting rapid regulation of postural leg muscles when subjects stand on a rigid floor (Lajoie et al, 1995) or on an unstable (rocking) surface (Solopova et al, 2003). The reason why Keck et al (1998) found conflicting results remains to be resolved.

In summary, the use of TMS to study the role of the cortex in the control of balance reactions still remains much in its infancy, but has the potential to provide new insight that will complement the knowledge gained from evoked-potential studies. However, attempts to apply single-pulse TMS during the balance reaction is likely to lead to difficulties in maintaining a stable stimulation site, as well as other methodological problems, which will be exacerbated when the balance reaction involves substantial body motion. These problems have led to an emerging interest in the use of image-guided repetitive TMS (administered prior to perturbation onset) as a possible tool to explore the influence of focal inhibition or facilitation of specific cortical regions on the control of balance reactions.

7. DISCUSSION

A number of dual-task studies support the view that balance-recovery reactions do indeed require cognitive resources. More complex reactions, such as stepping, appear to require more resources than reactions that do not involve limb movement. Competing demands for cognitive resources appear to primarily affect the later phases of the postural reactions, associated with the generation of peak ankle torque and subsequent restabilization (fixed-support reactions) or the planning of the foot-lift and/or limb trajectory (change-in-support reactions). Conversely, studies have consistently shown little or no effect on the earliest postural reaction at the ankle (the so-called "automatic postural response"). It remains to be resolved whether this reflects a truly automatic level of control that does not require cognitive resources (as suggested by visuomotor-tracking dual-task studies), or occurs because the CNS prioritizes allocation of cognitive resources to this phase of the postural reaction (as suggested by dual-task studies involving reaction-time probes).

In any case, it does appear that the CNS is normally able to rapidly switch attention and other cognitive resources to the task of balance recovery, when required. In older adults, however, this attention switching is delayed and a compromised ability to rapidly reallocate cognitive resources appears to degrade later phases of the postural reaction, e.g. slowing of peak ankle-torque generation during fixed-support reactions and reduction in the amplitude and duration of anticipatory postural adjustments during stepping reactions that required clearance of an obstacle.

With regard to visual attention, it appears that the CNS is able to use “stored” information about the environment to guide limb movements during balance-recovery reactions, and that this information is normally acquired and updated on an ongoing basis, prior to perturbation onset. This control strategy allows both vision and attention to be directed to other demands during the execution of the balance-recovery reaction.

Evoked-potential and transcranial magnetic stimulation (TMS) studies may ultimately help to identify the cortical structures that are involved in controlling balance-recovery reactions. Results to date from evoked-potential studies suggest that an early and robust N1 potential, centered over the frontal cortex, is related to detection of instability. Although initial TMS studies have produced conflicting results, one study has suggested that the early “automatic postural response” at the ankle is mediated, in part, by the motor cortex. Interestingly, the latency of the N1 potential (peak within ~100-200ms after perturbation onset) is likely too late to be involved in the earliest phase of the balance reactions, i.e. the APR, in which the latency of ankle-muscle activation occurs as early as 80ms after perturbation onset. This observation, which suggests that the APR is triggered and scaled at a sub-cortical level, appears to conflict with the TMS result suggesting early motor-cortex involvement. Clearly, more research is needed to resolve this issue.

The various experimental methods described in this review represent complementary approaches. Each approach has its own advantages and disadvantages. One major advantage of dual-task experiments is that they are relatively easy to perform and can allow inferences to be drawn regarding the functional nature of the cognitive demands. For example, the need for visuospatial processing in executing balance reactions can be inferred by comparing the effects of performing a visuospatial cognitive task (e.g. Brooks spatial-memory test (Kerr et al, 1985) with a non-visuospatial task (e.g. verbal recall). One limitation, however, is the inability to control or identify the switching of attention that can occur in the intervals between discrete cognitive-task responses. The tracking-task paradigm was designed to allow such attention switching to be identified, by requiring continuous cognitive-task performance and inferring that the appearance of significant tracking deviation marks the onset of the attention switching. The tracking task must be very carefully designed, however, to avoid inaccuracies that can arise if the tracking task is either too easy (allowing predictive control that can delay the appearance of perturbation-related tracking deviation) or too difficult (leading to poor tracking performance that may mask the appearance of perturbation-related tracking deviation). Use of reaction-time probes is another approach that can help to pinpoint the timing of the attentional demands, but this approach is not well suited to addressing the effect of more complex cognitive tasks. Another factor that can complicate interpretation of dual-task experiments is the need for some form of motor response in order to quantify the dual-task interference. As a result, the interference due to a backward counting task, for example, could be related to the motor demands of articulation (rather than the computational demands) (Yardley et al, 1999), and the interference due to a visuomotor tracking task could be related to the motor demands associated with the thumb movement (rather than the visuospatial processing demands of the tracking task).

Analysis of the eye movements associated with balance reactions allows very specific cognitive demands to be assessed, namely, changes in overt visual attention that are inferred by measuring changes in point of gaze. The connection between point of gaze and covert visual attention, involving the peripheral visual field, is more tenuous. While it is possible to determine whether a specific object lies within the known limits of the peripheral field of view at any given point in time, this does not necessarily imply that the subject attended to that object.

The most significant limitation associated with evoked-potential studies pertains to the need to average multiple trials in order to achieve adequate signal-to-noise ratio in the

EEG measurements (although it is sometimes possible to observe the large N1 component in single trials, as illustrated in Figure 8c). The need to average multiple trials may limit ability to study the single-trial responses that are often of most interest, e.g. the response evoked during the very first exposure to the perturbation. Repetition of large numbers of trials is also time-consuming and fatiguing, and hence limits the number of task conditions that can be tested. Moreover, this repetition paves the way for adaptive changes in the responses that may confound the findings (Horak, 1995; McIlroy and Maki, 1995). TMS has an advantage in that it does not require averaging of multiple trials, but current approaches suffer from problems in maintaining a stable stimulation site. However, the potential to combine "offline" repetitive TMS with image-guided localization may provide new opportunities to identify involved cortical loci with a high degree of confidence. Further work is needed to establish the full potential of this technique.

Potentially, by combining behavioral paradigms that can characterize cognitive demands (e.g. dual-task protocols, gaze measurements) with electrophysiological methods that can characterize cortical involvement (e.g. evoked potentials, TMS), future studies will be able to provide new insight into the brain structures that underlie normal postural behavior, as well as changes in balance control due to aging or disease. Although work to date has already provided much useful information, future work may benefit greatly by utilizing existing and emerging methodologies to better localize the involved cortical loci (e.g. dipole mapping of EEG data, image-guided rTMS). Future work is also likely to benefit by developing experimental paradigms that better simulate the challenges of controlling balance in daily life. This can involve more realistic simulation of "real-life" environments and situations in the laboratory. A complementary approach is to take advantage of emerging wireless technologies to study postural behavior in "real-life" settings. An important component of this focus on ecologic validity is the need to study the full range of balance-recovery reactions that occur in daily life. As is evident from this review, there has been considerable work devoted to fixed-support and stepping reactions; however, the cognitive demands and cortical contributions to the control of postural arm reactions have received much less attention.

In concluding, we would like to briefly note the clinical implications of this body of research. In terms of clinical balance assessment, dual-task protocols provide a simple and inexpensive opportunity to identify impairments in balance control that might otherwise not be evident. Similarly, dual-task protocols may be useful during intervention programs that aim to train improved balance-recovery reactions (Mansfield et al, 2007). In addition to the potential of providing additional diagnostic information, an appropriately-designed dual-task protocol could enhance the ecologic validity of the balance assessment. Daily life is unlikely to provide many opportunities to focus attention on responding to a forthcoming perturbation. Rather, the person is more than likely to be engaged in some form of ongoing cognitive and/or motor activity when loss of balance occurs, suddenly and unexpectedly. Dual-task approaches are already being used in conjunction with clinical balance tests (e.g. performing mental arithmetic during the “Timed Up and Go” test (Shumway-Cook et al, 2000)), and could find similar application during the clinical testing of balance reactions. Although this has yet to be established, it is possible that use of additional instrumentation, to record eye movements and cortical potentials and to apply TMS, may also provide useful information during clinical balance assessments; however, the expense of such instrumentation would likely limit application to major clinical centers.

8. ACKNOWLEDGMENTS

Studies by the authors that are described in this review were supported by grants from the Canadian Institutes of Health Research. The authors gratefully acknowledge assistance provided by Dr. Sylvia Quant and Amy Peters during the preparation of this manuscript.

9. REFERENCES

Ackermann H, Diener HC, Dichgans J (1986) Mechanically evoked cerebral potentials and long-latency muscle responses in the evaluation of afferent and efferent long-loop pathways in humans. Neurosci Lett 66: 233-238

Adkin A, Quant S, Maki BE, McIlroy WE (2006) Cortical responses associated with predictable and unpredictable compensatory balance reactions. Exp Brain Res 172: 85-93

Alexander NB, Mollo JM, Giordani B, Ashtonmiller JA, Schultz AB, Grunawalt JA, Foster NL (1995) Maintenance of balance, gait patterns, and obstacle clearance in Alzheimer's disease. Neurology 45: 908-914

Brauer SG, Woollacott M, Shumway-Cook A (2002) The influence of a concurrent cognitive task on the compensatory stepping response to a perturbation in balance-impaired and healthy elders. Gait Posture 15: 83-93

Brown LA, Shumway-Cook A, Woollacott MH (1999) Attentional demands and postural recovery: the effects of aging. J Gerontol 54A: M165-M171

Cejka C, Lee TA, McIlroy WE, Maki BE (2005) Gaze behavior associated with the response to an unexpected balance perturbation while walking in an unfamiliar environment. Gait Posture 21: S24

Chong RKY, Jones CL, Horak FB (1999) Postural set for balance control is normal in Alzheimer's but not in Parkinson's disease. J Gerontol 54: M129-M135

Dietz V (1992) Human neuronal control of automatic functional movements: Interaction between central programs and afferent input. Physio Rev 72: 33-69

Dietz V, Quintern J, Berger W (1984) Cerebral evoked potentials associated with the compensatory reactions following stance and gait perturbation. Neurosci Lett 50: 181-186

Dietz V, Quintern J, Berger W (1985a) Afferent control of human stance and gait: evidence for blocking of group I afferents during gait. Exp Brain Res 61: 153-163

Dietz V, Quintern J, Berger W, Schenk E (1985b) Cerebral potentials and leg muscle e.m.g. responses associated with stance perturbation. Exp Brain Res 57: 354-384

Dimitrov B, Gavrilenko T, Gatev P (1996) Mechanically evoked cerebral potentials to sudden ankle dorsiflexion in human subjects during standing. Neurosci Lett 208: 199-202

Duckrow RB, Abu-Hasaballah K, Whipple R, Wolfson L (1999) Stance perturbation-evoked potentials in old people with poor gait and balance. Clin Neurophysiol 110: 2026-2032

Ghafouri M, McIlroy WE, Maki BE (2004) Initiation of rapid reach-and-grasp balance reactions: is a pre-formed visuospatial map used in controlling the initial arm trajectory? Exp Brain Res 155: 532-536

Gordon R, Rzempoluck EJ (2004) Introduction to laplacian montages. American Journal of Electroneurodiagnostic Technology 44: 98-102

Horak FB (1995) Adaptation of automatic postural responses. In: J Bloedel, TJ Ebner, SP Wise (eds) Acquisition of Motor Behavior in Vertebrates, MIT Press, Cambridge,MA

Horak FB, MacPherson JM (1996) Postural orientation and equilibrium. In: J Shepard, L Rowell (eds) Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems, pp 255-292. Oxford University Press, New York

Keck ME, Pijnappels M, Schubert M, Colombo G, Curt A, Dietz V (1998) Stumbling reactions in man: influence of corticospinal input. Electromyography and Motor Control-Electroencephalography and Clinical Neurophysiology 109: 215-223

Kerr B, Condon SM, McDonald LA (1985) Cognitive spatial processing and the regulation of posture. J Exp Psychol 11: 617-622

King EC, Lee TA, Maki BE (2007) Does peripheral vision contribute to online control of grasping reactions evoked by unexpected perturbation when walking in an unfamiliar environment? Gait and Posture (suppl; in press)

Lajoie BA, Cody FWJ, Capaday C (1995) Cortical control of human soleus muscle during volitional and postural activities studied using focal magnetic stimulation. Exp Brain Res 103: 97-107

Lee TA, McKay SM, Peters AL, Maki BE (2007) Age-related differences in reach-to-grasp reactions and associated gaze behavior evoked by unexpected perturbation when walking in an unfamiliar environment. Gait and Posture (suppl; in press)

Macpherson JM, Fung J, Jacobs R (1997) Postural orientation, equilibrium, and the spinal cord. Advances in Neurology 72: 227-232

Maeda F, Keenan JP, Tormos JM, Topka H, Pascual-Leone A (2000) Interindividual variability of the modulatory effects of repetitive transcranial magnetic stimulation on cortical excitability. Exp Brain Res 133: 425-430

Maki BE (2007) Postural strategies. In: MD Binder, N Hirokawa, U Windhorst (eds) Encyclopedia of Neuroscience, Springer, New York (in press)

Maki BE, McIlroy WE (1997) The role of limb movements in maintaining upright stance: the "change-in-support" strategy. Phys Ther 77: 488-507

Maki BE, McIlroy WE (2005) Change-in-support balance reactions in older persons: an emerging research area of clinical importance. In: JM Furman, SL Whitney (eds) Neurologic Clinics, pp 751-783. Elsevier, Philadelphia

Maki BE, McIlroy WE, Fernie GR (2003) Change-in-support reactions for balance recovery: control mechanisms, age-related changes and implications for fall prevention. IEEE Engineering in Medicine and Biology Magazine 22: 20-26

Maki BE, Norrie RG, Zecevic A, Quant S, Kirshenbaum N, Bateni H, McIlroy WE (2001a) Initiation and execution of rapid postural reactions and stepping movements: which phases require visuospatial attention? In: J Duysens, BCM Smits-Engelsman, H Kingma (eds) Control of Posture and Gait, pp 573-576. International Society for Postural and Gait Research, Maastricht, Netherlands

Maki BE, Perry SD, Scovil CY, Mihailidis A, Fernie GR (2006) Getting a grip on stairs: research to optimize effectiveness of handrails. In: RN Pikaar, EAP Koningsveld, PJM Settels (eds) Proceedings IEA2006 Congress, pp 4669-4674 (article #778). Elsevier, Amsterdam

Maki BE, Zecevic A, Bateni H, Kirshenbaum N, McIlroy WE (2001b) Cognitive demands of executing rapid postural reactions: does aging impede attentional switching? NeuroReport 12: 3583-3587

Mansfield AM, Peters AP, Liu BA, Maki BE (2007) A perturbation-based balance training program for older adults: study protocol for a randomised controlled trial. BioMed Central Geriatrics (in press):

Massion J (1991) Movement, posture and equilibrium: interaction and coordination. Prog in Neurobiol 38: 35-56

McIlroy WE, Maki BE (1993) Do anticipatory postural adjustments precede compensatory stepping reactions evoked by perturbation? Neurosci Lett 164: 199-204

McIlroy WE, Maki BE (1994) The 'deceleration response' to transient perturbation of upright stance. Neurosci Lett 175: 13-16

McIlroy WE, Maki BE (1995) Adaptive changes to compensatory stepping responses. Gait Posture 3: 43-50

McIlroy WE, Maki BE (1999) The control of lateral stability during rapid stepping reactions evoked by antero-posterior perturbation: does anticipatory control play a role? Gait Posture 9: 190-198

McIlroy WE, Norrie RG, Brooke JD, Bishop DC, Nelson AJ, Maki BE (1999) Temporal properties of attention sharing consequent to disturbed balance. NeuroReport 10: 2895-2899

McKay SM, Peters AL, Scovil CY, Lee TA, Maki BE (2007) Do age-related deficits in visual processing predict impaired control of change-in-support balance-recovery reactions? Gait Posture (suppl; in press)

Muller MLTM, Redfern MS, Furman JM, Jennings JR (2004) Effect of preparation on dual-task performance in postural control. J Motor Behav 36: 137-146

Nashner LM, McCollum G (1985) The organization of human postural movements: A formal basis and experimental synthesis. The Behavioral and Brain Sciences 8: 135-172

Norrie RG, Maki BE, Staines WR, McIlroy WE (2002) The time course of attention shifts following perturbation of upright stance. Exp Brain Res 146: 315-321

Pashler HE, (1999) The Psychology of Attention, MIT Press, Cambridge, MA

Quant S, Adkin A, Staines WR, Maki BE, McIlroy WE (2004a) The effect of a concurrent cognitive task on cortical potentials evoked by unpredictable balance perturbations. BioMed Central Neuroscience 5: 18

Quant S, Adkin A, Staines WR, McIlroy WE (2004b) Cortical activation following a balance disturbance. Exp Brain Res 155: 393-400

Quant S, Maki BE, McIlroy WE (2005) The association between later cortical potentials and later phases of postural reactions evoked by perturbations to upright stance. Neurosci Lett 381: 269-274

Rankin J, Woollacott MH, Shumway-Cook A, Brown L (2000) Cognitive influence on postural stability: a neuromuscular analysis in young and elders. J Gerontol 55A: M112-M119

Redfern MS, Muller ML, Jennings JR, Furman JM (2002) Attentional dynamics in postural control during perturbations in young and older adults. J Gerontol 57: B298-B303

Schröger E (1996) A neural mechanism for involuntary attention shifts to changes in auditory stimulation. J Cognitive Neurosci 8: 527-539

Scovil CY, Zettel JL, King EC, Maki BE (2007) Stepping to recover balance in complex environments: is online visual control necessary or sufficient? Gait Posture (suppl; in press)

Shumway-Cook A, Brauer S, Woollacott MH (2000) Predicting the probability for falls in community-dwelling older adults using the Timed Up & Go test. Phys Ther 80: 896-903

Shumway-Cook A, Woollacott M, Kerns KA, Baldwin M (1997) The effects of two types of cognitive tasks on postural stability in older adults with and without a history of falling. J Gerontol 52A: M232-240

Solopova IA, Kazennikov OV, Deniskina NB, Levik YS, Ivanenko YP (2003) Postural instability enhances motor responses to transcranial magnetic stimulation in humans. Neurosci Lett 337: 25-28

Staines WR, McIlroy WE, Brooke JD (2001) Cortical representation of whole-body movement is modulated by proprioceptive discharge in humans. Exp Brain Res 138: 235-242

Stewart L, Ellisen A, Walsh V, Cowey A (2001) The role of transcranial magnetic stimulation (TMS) in studies of vision, attention and cognition. Acta Psychologica 107: 275-291

Taube W, Schubert M, Gruber M, Beck S, Faist M, Gollhofer A (2006) Direct corticospinal pathways contribute to neuromuscular control of perturbed stance. J Appl Physiol 101: 420-429

Ward NS, Franckowiak RS (2003) Age-related changes in the neural correlates of motor performance. Brain 126: 873-888

Wikswo JPJ, Gevins A, Williamson SJ (1993) The future of the EEG and MEG. Electroencephalog Clin Neurophysiol 87: 1-9

Woollacott M, Shumway-Cook A (2002) Attention and the control of posture and gait: a review of an emerging area of research. Gait Posture 16: 1-14

Yardley L, Gardner M, Leadbetter A, Lavie N (1999) Effect of articulatory and mental tasks on postural control. NeuroReport 10: 215-219

Zettel JL, Holbeche A, McIlroy WE, Maki BE (2005a) Redirection of gaze and switching of attention during rapid stepping reactions evoked by unpredictable postural perturbation. Exp Brain Res 165: 392-410

Zettel JL, McIlroy WE, Maki BE (2002) Can stabilizing features of rapid triggered stepping reactions be modulated to meet environmental constraints? Exp Brain Res 145: 297-308

Zettel JL, McIlroy WE, Maki BE (2005b) Gaze behavior and the modulation of triggered stepping reactions to meet environmental demands in older adults. Gait Posture 21: S12

Zettel JL, McIlroy WE, Maki BE (2005c) Visual behavior governing rapid stepping reactions in the presence of dynamic and unpredictable obstacles. Gait Posture 21: S21

Zettel JL (2006) Gaze behavior and visuospatial attention in compensatory stepping responses. Doctoral dissertation. University of Toronto, Toronto, Canada

Zettel JL, McIlroy WE, Maki BE (2007) Effect of competing attentional demands on perturbation-evoked stepping reactions and associated gaze behavior in young and older adults. Gait and Posture (suppl; in press)

10. FIGURE CAPTIONS

Figure 1: Balance-recovery strategies. Static postural equilibrium requires the body center of mass (COM) to be positioned over the base of support (BOS). The figures illustrate typical responses evoked by a perturbation (backward platform translation) that induces forward falling motion of the COM: **A.** feet-in-place reaction (ankle strategy); **B.** stepping reaction; **C.** reach-to-grasp reaction. Note the large increase in BOS that provides stabilization during the change-in-support strategies (stepping and reaching). The accompanying data plots display the: antero-posterior (a-p) center-of-pressure (COP) displacement; vertical ground-reaction forces (solid line = left leg; broken line = right leg); medial gastrocnemius (MG) EMG; medial deltoid (MD) EMG; and platform acceleration. Vertical lines indicate time of: perturbation onset (P); onset of the APR (early “automatic postural response”) (A); onset of the stepping response (S); foot off (FO); foot contact (FC); and handrail contact (HC). All displayed data were collected from a single healthy young-adult subject (unpublished data). COP and MG EMG are shown for the left leg (the stance leg during the stepping reaction); MD EMG is shown for the right arm (the arm used to grasp the rail in the reach-to-grasp reaction); EMGs are full-wave rectified. Note that the APR (initial MG burst) occurs in all three responses (prior to step initiation in **B**; in parallel with the initial MD burst that marks the initiation of the reach-to-grasp reaction in **C**).

Figure 2: Example results from dual-task studies showing the effect of responding to a sudden balance perturbation on performance of: **A.** a concurrent mental-arithmetic (counting backward by serial 3’s) task (adapted from Brown et al (1999)) and **B.** a concurrent auditory reaction-time task (adapted from Brauer et al (2002)). The arrows highlight the slowing in counting that occurred in older adults when using a stepping reaction to recover balance (**A**) and the large delay in auditory reaction-time that occurred when balance-impaired older adults stepped to recover balance (**B**).

Figure 3: Use of a reaction-time probe to assess attentional demands during different stages of the postural reaction. The arrows indicate the times at which the reaction-time stimulus was delivered, in relation to the onset of platform motion. The graph illustrates the delay in mean auditory reaction-time (young-adult subjects) when the auditory stimulus was delivered near time of perturbation onset (100ms before, 100ms after, or concurrent with perturbation onset), relative to responses to auditory stimuli delivered at later stages of the reaction (adapated from Redfern et al (2002)).

Figure 4: Visuomotor tracking-task paradigm developed by McIlroy, Maki and colleagues to study timing of attention switching. Panel **A** shows schematic drawings and photographs of the experimental set-up. Panels **B** and **C** show, on differing time scales, example tracking performance (young-adult subject) from a single perturbation trial (thick line) in relation to baseline tracking performance (95% confidence intervals) estimated from no-perturbation trials (thin lines). Panel **C** also shows EMG responses recorded at the ankle (tibialis anterior, TA) and in the tracking arm (medial deltoid, MD), as well as the platform acceleration. In panel **B**, the circle indicates the onset of tracking error that occurred in response to the perturbation that was delivered at the time indicated by the arrow. In panel **C**, note the complete pause in tracking (from T_1 to T_2) that began ~150ms after the "automatic postural response" (A) evoked in TA, ~300ms after perturbation onset (P). Note also the absence of any perturbation-evoked arm activation that might have interfered with tracking performance. Data are from McIlroy et al (1999) and Norrie et al (2002).

Figure 5: Effect of static environmental constraints on attention switching and gaze behavior during forward stepping reactions in young and older adults: **A.** experimental set-up showing the obstacle and step targets used to increase demands for accurate foot movement; **B.** frequency of downward gaze shift; and **C.** frequency of attention switching (as inferred from onset of significant tracking deviation; e.g. see Figure 4c). In **B** and **C**, only gaze shifts

and attention switches that occurred after perturbation onset and prior to foot contact were considered. Note the high frequency of attention switching and the low frequency of downward gaze shift. Note also that the older adults were somewhat more likely than the young to switch attention in the less demanding constraint conditions, and were most likely to look down when the obstacle was present whereas younger adults looked down most frequently when instructed to land the step foot on the target line. Data are from Zettel et al (2005a; 2005b; 2006).

Figure 6: Experimental set-up used to study the effect of unpredictable environmental constraints on gaze behavior during forward stepping reactions in young and older adults: **A.** schematic drawing depicting the range of motion of the four motor-driven obstacle movers that were mounted on the motion platform; **B.** photograph showing the platform surface when all obstacles are in the retracted position (no constraints on foot movement); **C.** photograph showing the final obstacle configuration (prior to perturbation onset) used in the study by Zettel et al (2005c); **D.** and **E.** photographs showing the two obstacle configurations used in the study by Scovil et al (2007). The obstacle configuration in **C** required subjects to execute the forward step reaction using the left (non-dominant) leg; the configurations in **D** and **E** required the step foot to be directed through the slot. In both studies, the perturbation direction (forward, backward, left or right) was always unpredictable to the subject. In the study by Zettel et al, subjects only performed a single trial and the final obstacle configuration was arrived at ~2s prior to perturbation onset (after ~25s of intermittent unpredictable motion of all four obstacles). In the study by Scovil et al, liquid crystal goggles were used to occlude vision either prior to or after perturbation onset, so that subjects either were or were not allowed to view the obstacle configuration prior to the perturbation; the initial stance width was varied between trials (in addition to the random variation in slot location) to further reduce any capacity to “remember” the required foot trajectories.

Figure 7: Experimental set-up used by Maki and colleagues (Cejka et al, 2005; King et al, 2007; Lee et al, 2007; McKay et al, 2007) to study the attentional demands associated with reach-to-grasp reactions evoked by an unexpected perturbation while ambulating in an unfamiliar environment: **A.** schematic drawing of the extended (2x6m) motion platform, configured to simulate a realistic living environment; **B.** photograph of the view that the subject sees upon opening the door at the start of the trial. The subject is given a distraction task that requires walking to the end of the platform (e.g. make a phone call, using the phone located on the desk); the platform is triggered by pressure switches to move unexpectedly forward or backward when the subject steps on the mat adjacent to the handrail.

Figure 8: Cortical potentials evoked by sudden balance perturbation (young-adult subjects): **A.** temporal features; **B.** topographic distribution; **C.** influence of predictability of perturbation timing. Panel **A** shows the EEG (Cz electrode site) and tibialis-anterior EMG (feet-in-place balance reaction) evoked by forward platform translation (single subject, average of 32 trials). Note the large negative peak (N1) that occurs ~200ms after perturbation onset (P), the positive peak (P2) that follows the N1, and the absence of any positive peaks prior to the N1 (i.e. the small P1 peak that has been reported in some studies). Panel **B** illustrates how the N1 potential was most pronounced at frontocentral electrode sites during a simulated balance-perturbation task involving use of a foot pedal to stabilize an inverted-pendulum load (grand average of 8 subjects, ~30 trials per subject). Panel **C** compares the averaged EEG responses (single subject, 30 trials) evoked by forward trunk-push perturbations when perturbation onset timing was either predictable or unpredictable, and also shows a single-trial response to an unexpected perturbation (“surprise trial”). Note that the N1 peak emerged only when the perturbation was unpredictable. Data are from Quant et al (2004a; 2004b) and Adkin et al (2006).

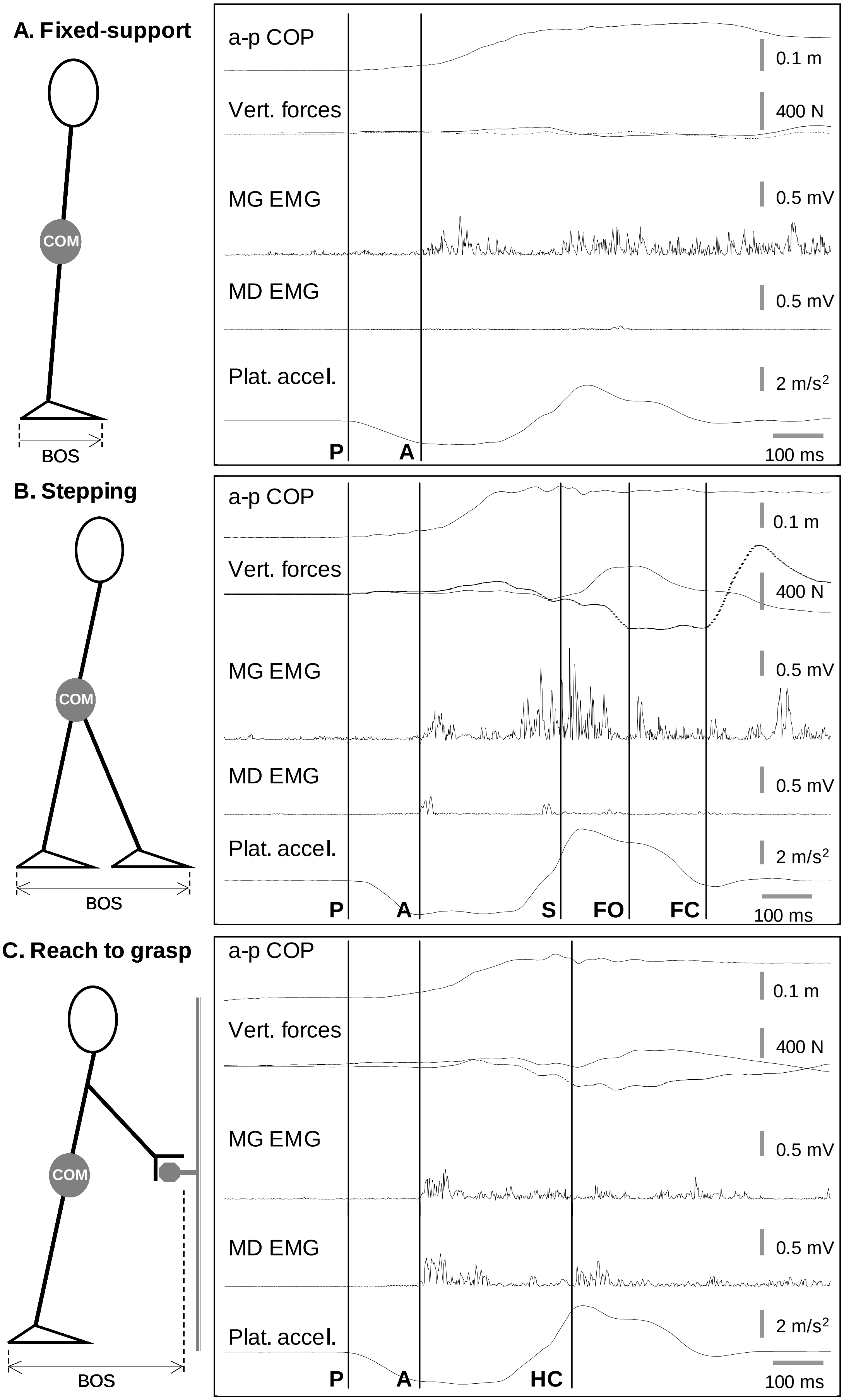
A. Fixed-support
COM
BOS
a-p COP
0.1 m
Vert. forces
400 N
MG EMG
0.5 mV
MD EMG
0.5 mV
Plat. accel.
2 m/s^2
P
A
100 ms
B. Stepping
COM
BOS
a-p COP
0.1 m
Vert. forces
400 N
MG EMG
0.5 mV
MD EMG
0.5 mV
Plat. accel.
2 m/s^2
P
A
S
FO
FC
100 ms
C. Reach to grasp
COM
BOS
a-p COP
0.1 m
Vert. forces
400 N
MG EMG
0.5 mV
MD EMG
0.5 mV
Plat. accel.
2 m/s^2
P
A
HC
100 ms

Figure 1

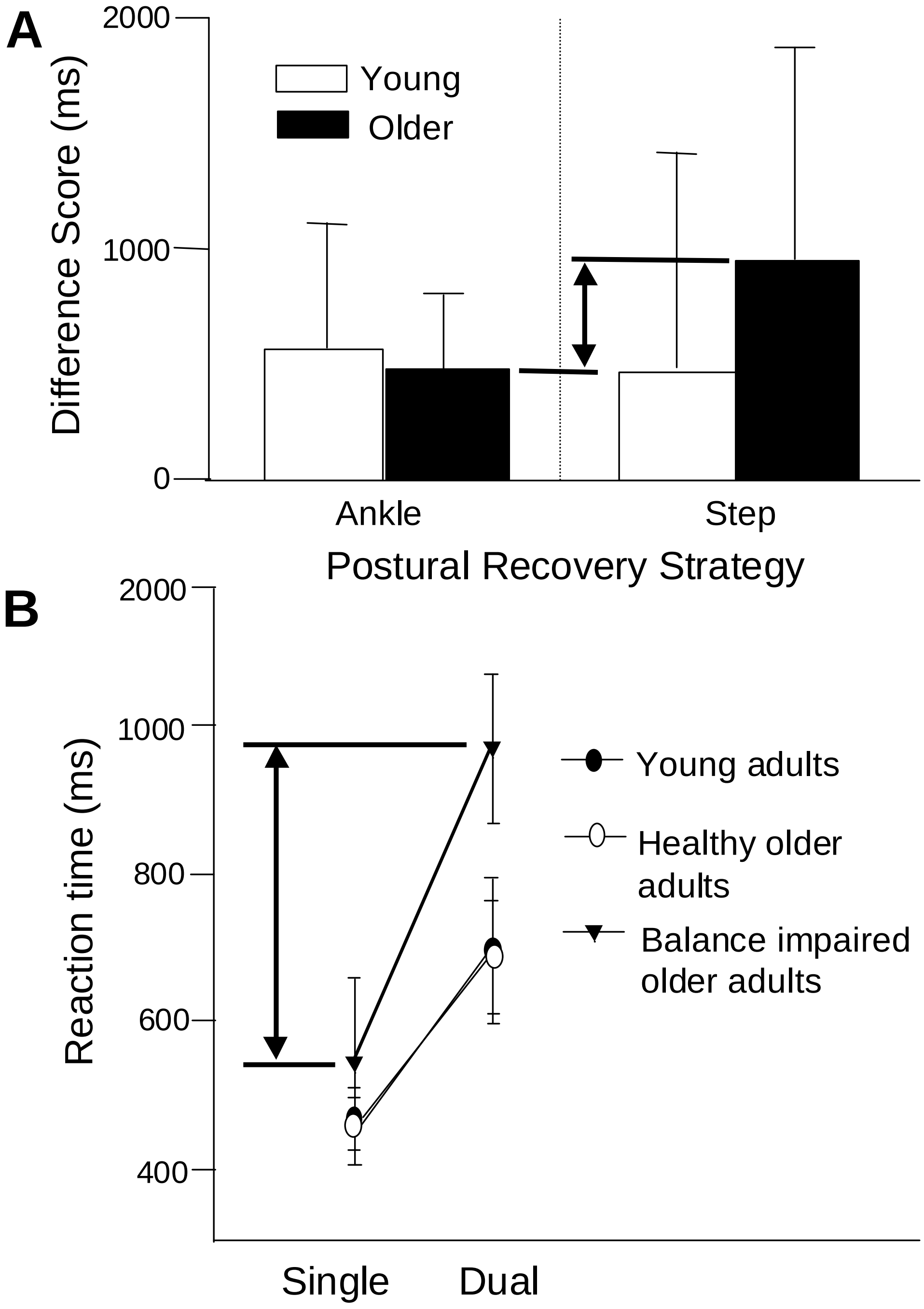
A
2000
1000
0
Difference Score (ms)
Young
Older
Ankle
Step
Postural Recovery Strategy
B
2000
1000
800
600
400
Reaction time (ms)
Young adults
Healthy older adults
Balance impaired older adults
Single
Dual

Figure 2

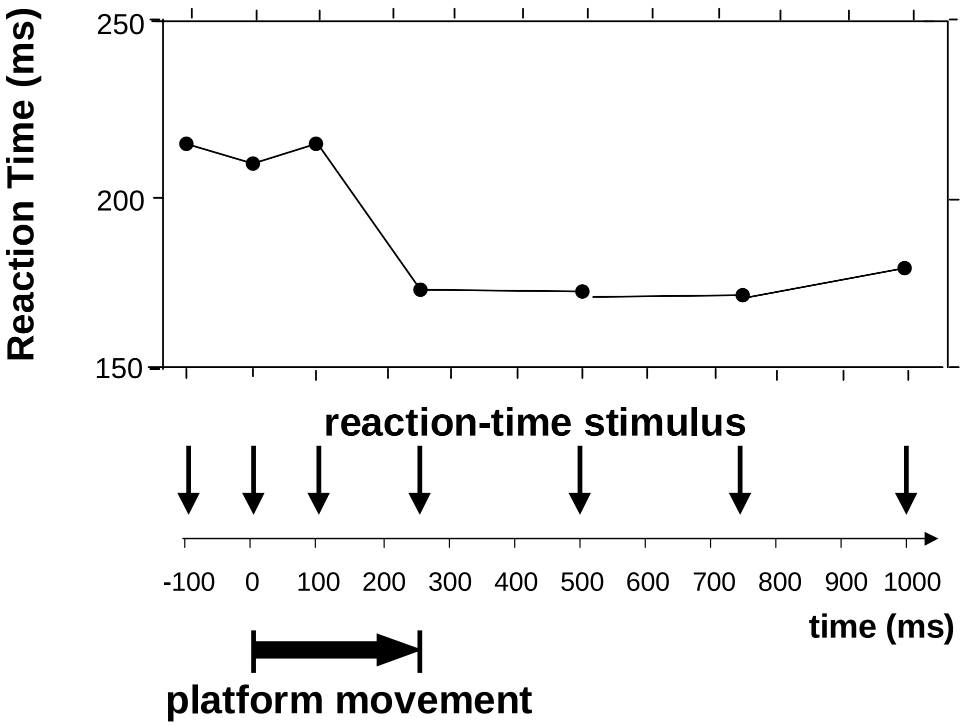
Reaction Time (ms)
250
200
150
reaction-time stimulus
-100
0
100
200
300
400
500
600
700
800
900
1000
time (ms)
platform movement

Figure 3

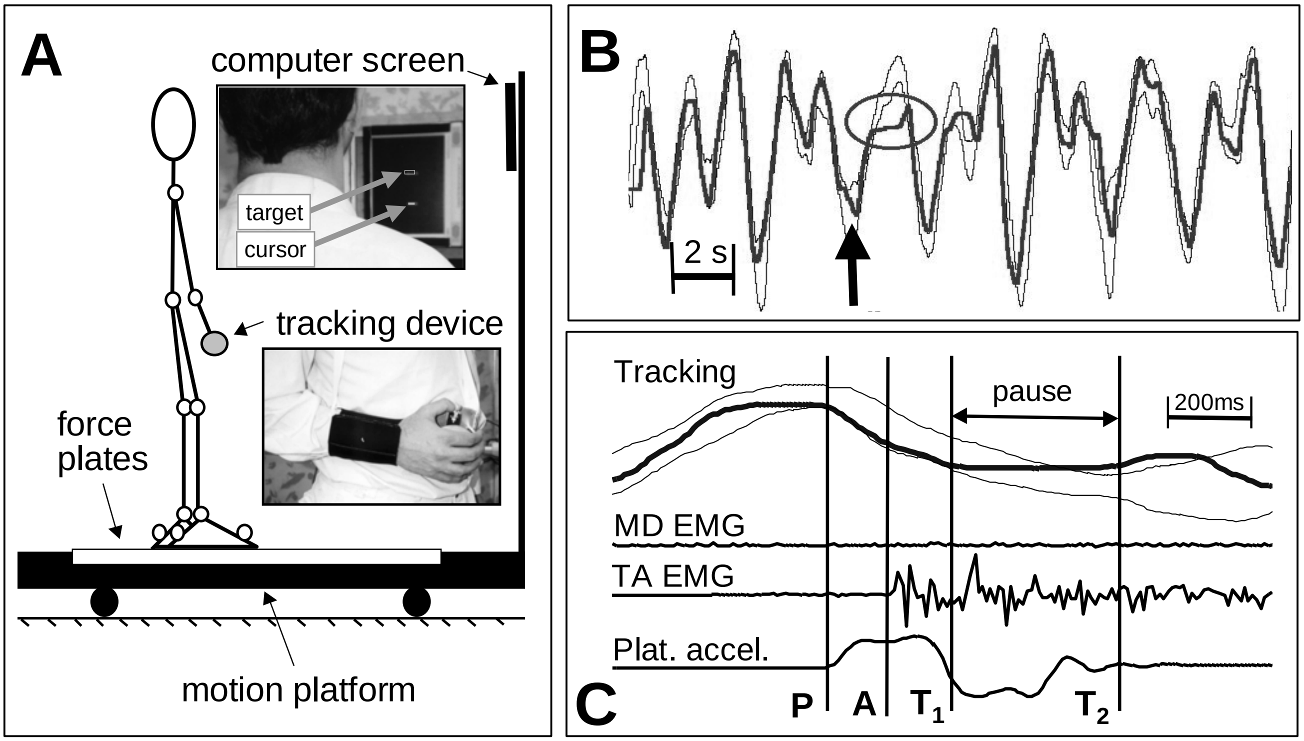
A
computer screen
target
cursor
tracking device
force plates
motion platform
B
2 s
Tracking
pause
200ms
MD EMG
TA EMG
Plat. accel.
C
P
A
T1
T2

Figure 4

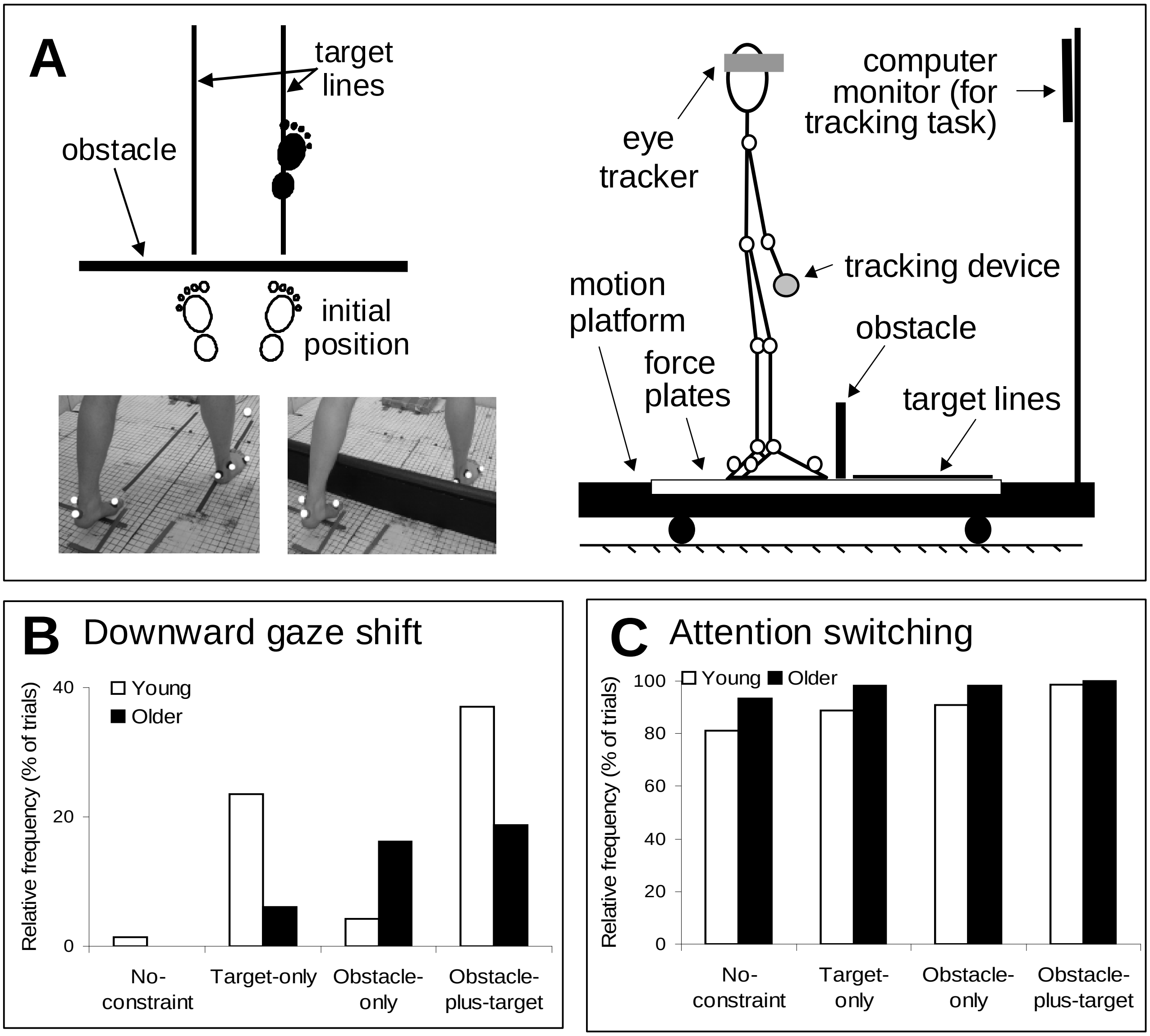
A
target lines
obstacle
initial position
eye tracker
computer monitor (for tracking task)
tracking device
motion platform
force plates
obstacle
target lines
B
Downward gaze shift
Relative frequency (% of trials)
40
20
0
☐ Young
■ Older
No-constraint
Target-only
Obstacle-only
Obstacle-plus-target
C
Attention switching
☐ Young ■ Older
Relative frequency (% of trials)
100
80
60
40
20
0
No-constraint
Target-only
Obstacle-only
Obstacle-plus-target

Figure 5

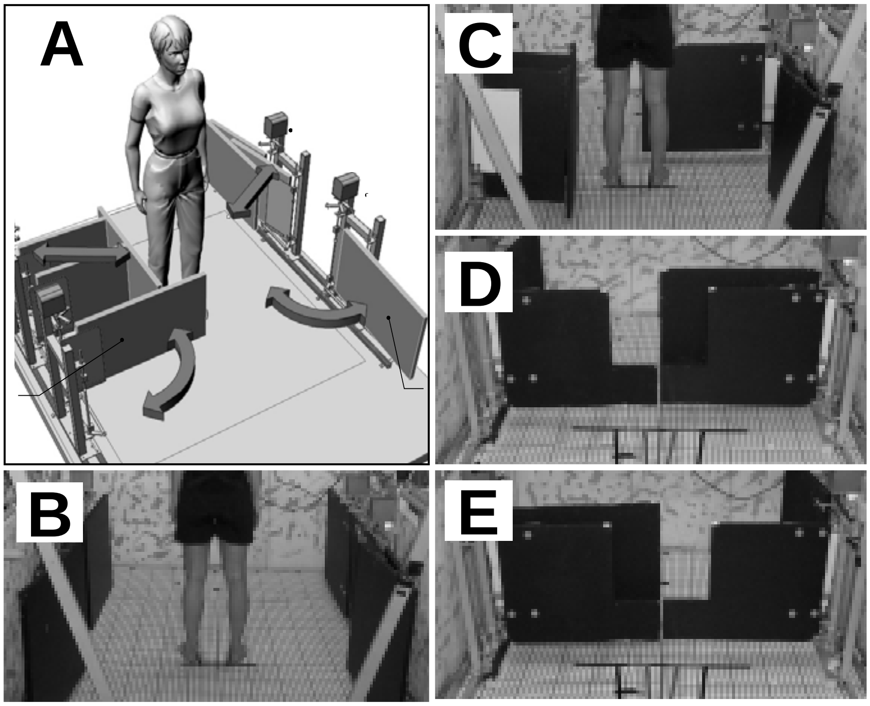

Figure 6

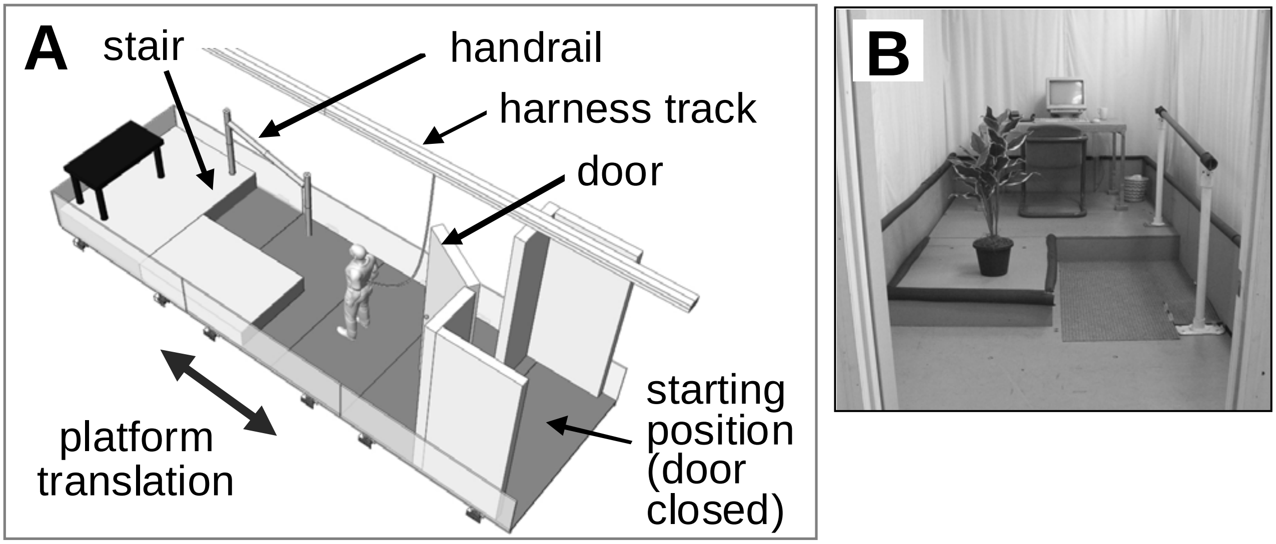
A
stair
handrail
harness track
door
starting position (door closed)
platform translation
B

Figure 7

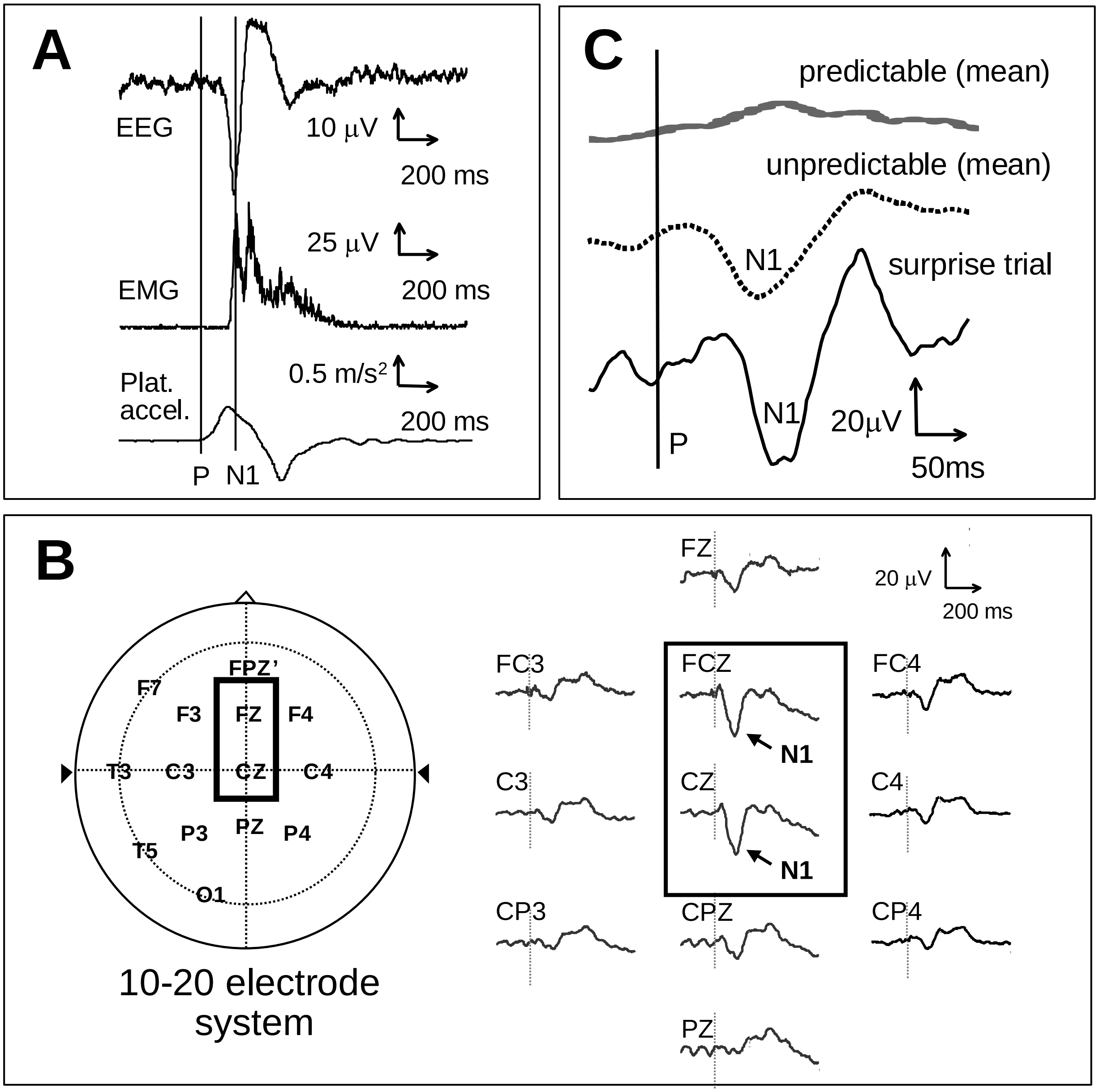
A
EEG
10 μV
200 ms
EMG
25 μV
200 ms
Plat. accel.
0.5 m/s²
200 ms
P
N1
C
predictable (mean)
unpredictable (mean)
N1
surprise trial
N1
20μV
50ms
P
B
FPZ’
F7
F3
FZ
F4
T3
C3
CZ
C4
P3
PZ
P4
T5
O1
10-20 electrode system
FZ
20 μV
200 ms
FC3
FCZ
FC4
N1
C3
CZ
C4
N1
CP3
CPZ
CP4
PZ

Figure 8