Neural markers of proactive and reactive cognitive control are altered during walking: A Mobile Brain-Body Imaging (MoBI) study★

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Abstract

The processing of sensory information and the generation of motor commands needed to produce coordinated actions can interfere with ongoing cognitive tasks. Even simple motor behaviors like walking can alter cognitive task performance. This cognitive-motor interference (CMI) could arise from disruption of planning in anticipation of carrying out the task (proactive control) and/or from disruption of the execution of the task (reactive control). In young healthy adults, walking-induced interference with behavioral performance may not be readily observable because flexibility in neural circuits can compensate for the added demands of simultaneous loads. In this study, cognitive-motor loads were systematically increased during cued task-switching while underlying neurophysiologic changes in proactive and reactive mechanisms were measured. Brain activity was recorded from 22 healthy young adults using 64-channel electroencephalography (EEG) based Mobile Brain/Body Imaging (MoBI) as they alternately sat or walked during performance of cued task-switching. Walking altered neurophysiological indices of both proactive and reactive control. Walking amplified cue-evoked late fontal slow waves, and reduced the amplitude of target-evoked fronto-central N2 and parietal P3. The effects of walking on evoked neural responses systematically increased as the task became increasingly difficult. This may provide an objective brain marker of increasing cognitive load, and may prove to be useful in identifying seemingly healthy individuals who are currently able to disguise ongoing degenerative processes through active compensation. If, however, degeneration continues unabated these people may reach a compensatory limit at which point both cognitive performance and control of coordinated actions may decline rapidly.

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1. Introduction

The integrity of cognitive control processes is crucial to successful preparation for and execution of behaviors (Espy, 2004; Miller and Cohen, 2001; Diamond, 2013; Lehto et al., 2003; Miyake et al., 2000). The Dual-Mechanisms of Control theory postulates separate control mechanisms underlying preparatory processes, which bring the system to a state of readiness in advance of an anticipated event (proactive control), and processes which operate on an as-needed basis following event onset (reactive control) (Braver et al., 2009, 2012, 2007; Paxton et al., 2008). As the number and difficulty of ongoing tasks increases, even young healthy individuals will approach limits on available cognitive resources and behavioral performance can decline (Marois and Ivanoff, 2005). For instance, simultaneous walking can both interfere with, and suffer interference from, ongoing cognitive task performance (Plummer et al., 2013). The notion that walking might have a detrimental effect on cognitive tasks (and vice versa) may seem somewhat counterintuitive, since we are inclined to think of walking as an automatic process that requires little, if any, cortical control. However, during walking, there is a constant influx of sensory information conveying critical updates about environment, heading direction, speed and potential hazards. Additional cognitive load occurs as a result of the necessary planning, adjustment and execution of motor commands, and corresponding gait corrections. Such simultaneous sensory and motor processes tax resource availability and allocation, and if resources are inadequate or inadequately distributed, both cognitive processing and gait stability are often degraded (Al-Yahya et al., 2011; Tomporowski and Audiffren, 2014; Sheridan et al., 2003; Montero-Odasso et al., 2012 a, 2012 b, 2017; Woollacott and Shumway-Cook, 2002).

Cognitive-motor performance and gait disturbances have been reported by some studies (Al-Yahya et al., 2011; Tomporowski and Audiffren, 2014; Sheridan et al., 2003; Montero-Odasso et al., 2012 a, 2012 b, 2017; Woollacott and Shumway-Cook, 2002; Sheridan and Hausdorff, 2007; Muir et al., 2012), yet others report stabilization of gait and performance benefits under low cognitive-motor loads (Decker et al., 2016, 2012; Hamacher et al., 2019 a; Verrel et al., 2009; Fearon et al., 2021). A dual-process framework of attentional redirection and cross-domain capacity limited resource competition is one way to reconcile these seemingly conflicting observations of facilitation and costs (Decker et al., 2016; Verrel et al., 2009; Lövdén et al., 2008). Low attentional demands shift overt focus away from motor processes. As cognitive control of gait is reduced, automaticity increases, reducing stride variability (Hamacher et al., 2019 a; Hausdroff, 2005). Progressively increasing difficulty eventually causes cognitive-motor demands to exceed resource capacity limits, overshadowing any benefits of increased gait automaticity and attentional focus on the cognitive task (Woollacott and Shumway-Cook, 2002; Schäfer et al., 2006; Li and Lindenberger, 2002).

Substantial progress has been made in characterizing alterations of brain dynamics during cognitive-motor tasks and spatial navigation (Banaei et al., 2017; Nenna et al., 2020; Protzak and Gramann, 2021; Cortney Bradford et al., 2019; Bradford et al., 2016; Lau et al., 2014; Reiser et al., 2019), yet neurophysiological underpinnings of altered performance have not been established. Studies using functional near infrared spectroscopy (fNIRS) to explore neural substrates of cognitive-motor interactions identified increased activity in prefrontal cortex (PFC) during combined cognitive and motor tasks (Holtzer et al., 2011; Al-Yahya et al., 2016), indicating increased recruitment of fronto-cortical mechanisms to handle the increased load of walking while also performing a cognitive task (Miller and Cohen, 2001; Braver et al., 2009; Widge et al., 2019; Botvinick and Cohen, 2014; Botvinick and Braver, 2015; Power and Petersen, 2013; Cole and Schneider, 2007). DeSanctis and colleagues used Mobile Brain-Body Imaging (MoBI) techniques (De Sanctis et al., 2014; Malcolm et al., 2015; Malcolm et al., 2018; Malcolm et al., 2019; Gramann et al., 2014, 2010) to investigate effects of simultaneous walking on two event-related potential (ERP) indices of cognitive control: the fronto-central N2 and centro-parietal P3 (Karayanidis and Jamadar, 2014; Jamadar et al., 2015). The amplitude of the fronto-central N2 was smaller, and the topography of the P3 shifted anteriorly, when participants performed a response inhibition task while walking on a treadmill compared to sitting (De Sanctis et al., 2014; Malcolm et al., 2015) (c). In a study of overground walking, P3 amplitude evoked by a visual discrimination task was reduced during simultaneous walking (Nenna et al., 2020). Anterior cingulate cortex (ACC), a major generator of the N2 component (Dias et al., 2003, 2006), is a critical hub in cognitive control networks (Botvinick and Braver, 2015; Power and Petersen, 2013; Cole and Schneider, 2007; Carter and van Veen, 2007; O'Connell et al., 2007; Niendam et al., 2012). DeSanctis interpreted these walking-related ERP modulations as a transition to less automatic, more effortful processing during simultaneous walking, reflecting more extensive engagement of cognitive control networks.

Task-switching while over-ground walking or navigating an obstacle course has demonstrated cue-evoked parietal P2, N2, and P3 amplitudes relative to standing (Reiser et al., 2019). No amplitude differences were observed when comparing the walking and obstacle course conditions, suggesting progressive increases to motor load did not cause further reductions in cue-evoked P2, N2, or P3 amplitudes, and cue- and target evoked frontal theta power (Reiser et al., 2019). However, the obstacle course consisted of three different obstacles, requiring a broad range of motor behaviors which may have posed inconsistent local fluctuations in cognitive-motor loads.

Although these previous studies identified changes to neural activity linked to cognitive control during an ambulatory task (De Sanctis et al., 2014; Malcolm et al., 2015, 2018; De Sanctis et al., 2012), the extent to which neurophysiological mechanisms underlying proactive and reactive control are respectively altered by movement is not yet understood. Here, a cued task-switching design was deployed to specifically examine changes to proactive and reactive control processes during walking (Fig. 1). This design dissociates proactive and reactive neurophysiological responses into a cue-target interval (CTI) and a post-target interval (PTI) respectively (Braver, 2012; Karayanidis and Jamadar, 2014; Kopp et al., 2014; Meiran, 1996; Foxe and Simpson, 2005; Foxe et al., 2005). High-density EEG captured neural activity of the separated cue-evoked proactive processes and target

stimulus-evoked reactive processes and how these changed during walking (Rugg and Coles, 1995; Czernochowski, 2015).

In addition to the distinction between proactive and reactive control, a second benefit to this approach is the comparison of trials with and without attention-switching requirements, permitting comparison of walking-related changes during greater and lesser cognitive load. In 'pure' blocks, participants performed only one of two discrimination tasks (either 'Task A' or 'Task B'). In 'mixed' blocks, participants switched between tasks as instructed by a cue ('Task A' and 'Task B' performed in same block; Fig. 1, see Methods for details). Mixed blocks are further separated into trials on which the rules remain the same as on the previous trial (mixed repeat trials), or trials on which the rules are changed (switch trials). Mixed blocks possess relatively greater complexity as cognitive control demands are increased (Rondeel et al., 2015; van der Wel and van Steenbergen, 2018) due to greater requirements of working memory, cognitive flexibility (Wylie et al., 2009), and suppression of competing task information evoked by irrelevant stimulus features (Wylie et al., 2004). Performance measures often differentiate block and trial types, with lower accuracy and slower responses on mixed block trials relative to pure block trials ("mixing costs "), and further reductions in performance on switch trials relative to mixed repeat trials ("switch costs ") (Wylie and Allport, 2000). The result is a progressive addition of cognitive control demands and a unique set of proactive and reactive control responses across the three trial types. We hypothesized that changes to proactive and reactive control mechanisms would depend on cognitive load due to both variable demands arising from the task-switching design and from simultaneous sensory-motor demands of walking. To test this hypothesis, ERPs evoked while sitting and walking were compared across trials with and without attention switching requirements at intervals corresponding to proactive and reactive neural processes sensitive to task-switching demands.

In the context of cued task-switching, there are well-defined ERP indices of both proactive and reactive control. The cue-evoked centroparietal positivity (sometimes termed *switch positivity*) and sustained frontal negativity (*pre-target negativity*) are ERP indices of proactive processes which sustain task representations in advance of the demanding event and signal task preparedness. Similarly, target-evoked N2 and P3 components are ERP indices of reactive processes mediating inhibitory control, task retrieval, and interference monitoring (Karayanidis and Jamadar, 2014; Jamadar et al., 2015). The centro-parietal positivity emerges ~300 ms after cue onset, is typically largest on switch trials, and has been correlated with activity in posterior parietal cortex (PPC) (Karayanidis and Jamadar, 2014; Karayanidis et al., 2009, 2010, 2011a; Gajewski et al., 2018; Jamadar et al., 2010). The 'sustained frontal negativity' is observed in tasks with a sufficiently long CTI (600–1000 ms), and has been correlated with dorsolateral prefrontal cortex (DLPFC) activation (Rosahl and Knight, 1995). There is some evidence that this sustained negativity is enhanced during switch trials (Astle et al., 2008), but it has also been reported that it is enhanced during mixed repeat trials (Gajewski et al., 2018). Both centro-parietal positivity and sustained frontal negativity are long and slow potentials which complement the sustained activations in PPC and DLPFC during proactive control states (Braver, 2012; Jamadar et al., 2015; Irlbacher et al., 2014). In the PTI, the amplitude of the fronto-central N2 tends to increase, whereas amplitude of the P3 tends to decrease as cognitive task load increases from the

simple pure trials to more complex mixed repeat trials, and increases further during switch trials (Jamadar et al., 2015). The N2 and P3 processes reflect activation of ACC, SMA, PPC, and fronto-polar regions within a broad hypothesized reactive control network (Jamadar et al., 2015; Irlbacher et al., 2014; Iannaccone et al., 2015).

Characterizing changes in brain activations that occur as conditions for task execution are altered is key to understanding how neural resources are marshaled as cognitive demands vary. Operating in complex environments may compel redistribution of neural resources at the cost of lower priority processes. In task switching, preparedness depends on the time provided to prepare (Rogers and Monsell, 1995), but likely also availability of neural resources for proactive processes over that interval. As ambulation, error correction, and hazard avoidance are added to a task, scarcer resource availability may restrict the opportunity for proactive control processes to occur. If proactive control were reduced, successful task completion would require more reliance on reactive control processes. We hypothesized progressive increases to cognitive-motor load would identify a "tipping point " beyond which a shift away from proactive processing towards a more reactive mode occurs. We predicted reductions in the amplitude of the cue-evoked sustained frontal negativity, cue-evoked centro-parietal positivity, target-evoked N2, and target-evoked P3 would indicate degradation of proactive processes and a shift to a reactive control mode. Characterizing this point may yield a novel neurophysiological benchmark for dynamic evaluation and projection of cognitive health.

2.   Materials and methods

2.1.   Participants

22 young adults (19–22 years old, mean age = 20.18 +/− 0.80 years, 11 male, 11 female) completed the cued task-switching experiment, providing the data analyzed in this report. All participants provided written informed consent, reported no diagnosed neurological conditions, no recent head injuries, normal or corrected-to-normal vision, and that they were not suffering experience post-concussive syndrome. All procedures were approved by the University of Rochester Institutional Review Board (STUDY00001952). Participants were paid $15/h for time spent in the lab.

2.2.   Stimuli and task

Participants performed the cognitive task while either sitting, or walking on a treadmill (Tuff Tread, Conroe, TX, USA). Each trial comprised a 100 ms cue, a 650 ms cue-target interval (CTI), a 100 ms target stimulus, and a 1000–1200 ms post target interval (PTI). A central-fixation cross was held on-screen continuously throughout each block. All visual task elements were projected on a screen 2.2 m (during seated blocks) in front of the participant. A black or white annulus encircling the central-fixation cross served as a cue on each trial, instructing participants to perform the spatial frequency discrimination or the orientation discrimination task respectively. Target stimuli comprised two bivalent images (differing in both orientation, and spatial frequency) presented to the left and right of the central fixation cross. Based on the location of the treadmill, the target eccentricity was 6.4° during sitting blocks. Trials in which two identical stimuli were presented ("replace trials

") occurred pseudorandomly throughout both pure and mixed blocks of the experiment. Target stimuli pairs were pseudorandomly selected from a 5×5 matrix of images (Fig. 1 B) to ensure incongruent task response mappings to the left- and right-hand response devices (2 Nintendo Switch Joy-Con TM controllers). Two stimuli representing the pairing of the greatest rotation with the highest spatial frequency, and the pairing of the least rotation with the lowest spatial frequency were in-eligible for selection on any non-replace trial, leaving a total of 200 possible stimulus pairings. Cues were delivered during both pure blocks (non-informative) and mixed blocks (informative). Cues would repeat a minimum of 4 times, after which the probability of a cue switch would increase on each subsequent trial. A maximum of 6 cue repetitions (1 switch trial + 5 repeats) were permitted. A minimum of 4 pure blocks were administered, 2 seated, 2 walking. A minimum of 10 mixed blocks were administered (5 seated, 5 walking). 2 walking only blocks (walking without performing the cognitive task) were also administered at pseudorandom intervals. A central fixation cross was held on screen during walking only blocks, but subjects did not perform a cognitive task. Walking and Sitting blocks were selected pseudorandomly, such that a maximum of 3 sitting or walking blocks could occur consecutively.

2.3. Procedure

Participants performed orientation discrimination and spatial frequency discrimination tasks in pure and mixed blocks while either sitting or walking on a treadmill at a comfortable speed. Participants also completed two walking only blocks. Participants and research personnel collaboratively determined a walking speed that was comfortable for the participant at the beginning of the experiment (mean speed = 1.18 m/s +/− 0.0441). The same walking speed was used in each walking block. Experiment block lasted 4–6 min. Short breaks occurred between every block (1–3 min) during which snacks or water was provided at participant request. Longer breaks could be taken at the participant's request. Each experiment was conducted in a single session lasting fewer than 5 h. Participants were guided through a training block with target duration increased to 8 s to permit feedback on selected responses provided by a research coordinator. Response feedback was not provided during the recorded experimental blocks. The instructions provided for the orientation discrimination task ('Task A') were to select the target stimulus image rotated further clockwise using the response devices. Participants were instructed that a stimulus with vertical lines represented a target stimulus image that was not rotated at all, horizontal lines represented maximal rotation, and that target stimuli would only be rotated between 0 and 90°. In the spatial frequency discrimination task ('Task B') participants were instructed to select the target stimulus image with higher spatial frequency using the response devices. 2 consecutive pure angle discrimination blocks (1 seated, 1 walking) and 2 consecutive pure spatial frequency (1 seated, 1 walking) discrimination blocks were performed, during which participants were instructed that the cue color did not provide performance feedback, or any prospective information beyond indicating an upcoming trial. Cue color-task mappings were revealed prior to the first mixed block and reminders were provided throughout the experiment. Experimental block consisted of 150 trials, 6 of which were replace trials occurring pseudorandomly. A minimum of 4 pure blocks (2 seated, 2 walking) and 10 mixed blocks (5 seated, 5 walking) was set for dataset inclusion in subsequent analyses.

2.4. Behavioral measure analysis

The response accuracy (d') and response times for trials performed in pure and mixed blocks were compared to obtain mixing costs. Switching costs were assessed by comparing mixed repeat and switch trials. Responses were considered valid if they occurred in the window 200–1000 ms following target stimulus onset. Trials in which no response was provided were excluded from analyses. D-prime, a signal detection measure, was used to assess response accuracy and calculated according to the following equation:

$$d' = \frac{1}{\sqrt{2}}[z_{Hit} - z_{False\ Alarm}]$$

In two-alternative forced choice experiments the classification of "hits ", and "false alarms " is arbitrary (Macmillan and Creelman, 2004). Here, "hits " were defined as trials in which the "correct " target stimulus image fell on the left side and the left response device was selected. "False alarms " were defined as trials in which the "correct " target stimulus image fell on the right side, but the left response device was selected. Altering these classifications does not change resultant d' values. Statistical analyses for performance measures were conducted using two 3×2 ANOVAs with factors of trial type (pure, mixed repeat, or switch) and physical condition (sitting or walking). Participant d' values and mean response times were used as dependent measures. Tukey's honest significant differences (HSD) test was used for post hoc analyses of switch costs. Significance threshold was set at $\alpha = 0.05$.

2.5. Gait recording and analysis

Kinematic data were recorded at 360 Hz using an optical motion capture system (Optitrack Prime 41 cameras, Motive v2.1 software, Natural Point Corvallis, OR, USA). 41 reflective markers were placed over anatomical landmarks on mocap suits worn by participants. In accordance with the "Baseline + Hinged Toe " default markerset. 4 markers were placed on each foot (posterior of the calcaneus, tip of the second distal phalanx, distal end of the first metatarsal, and distal end of the fifth metatarsal)and these were used to measure stride length, stride length variability, stride time, and stride time variability.

Processing and analysis of kinematic data was performed using MATLAB 2019b (Mathworks, Natick, MA, USA). Motion capture data from each walking block was lowpass filtered at 6 Hz with a 2nd order, zero-phase Butterworth filter. Intervals of marker occlusion were interpolated. Strides were excluded from analysis if a heel marker was occluded for longer than 1 gait cycle. The filtered signal was copied, and filtered again using a 25 point moving average to smooth remaining artifact. Automatic peak detection identified extreme horizontal values coincident with vertical movement onset and offset in the antero-posterior plane. Resultant points were classified as heel strikes and lifts in the 6 Hz lowpass filtered data. Review of motion capture confirmed timing of heel strikes and lifts.

1 participant was excluded from gait analysis due to recording equipment error. Walking data from the remaining 21 subjects was classified as walking only, walking during a pure block, or walking during a mixed block. A minimum of 200 consecutive strides was required for a block to be included in analysis. Stride length was extracted by summing the

horizontal distance between opposite heel markers at heel lifts and subsequent heel strikes. Stride time was measured as time elapsed between two consecutive heel strikes by the same foot. Coefficient of variation (CV% = (SD/mean) × 100) was used for measures of stride variability (Hausdroff, 2005). 1-way repeated measures ANOVA with the factor block type (walking only, pure, mixed) compared mean stride length, stride time, stride length variability, and stride time variability. When appropriate, Greenhouse-Geisser correction was used to account for violation of the assumption of sphericity. Tukey's HSD was used for post-hoc analysis and effect sizes were measured using Cohen's d.

2.6. EEG recording and pre-processing

EEG was recorded from 64 channels following the International 10–20 system. EEG was continuously collected and digitized at 2048 Hz throughout the duration of the experiment (BioSemi ActiveTwo, Amsterdam, The Netherlands). EEG data were streamed via LabStreamingLayer (LSL) to a computer along with task-event, and motion capture data streams. EEG data were visually inspected, and data corresponding to block intermissions was removed. EEG was bandpass filtered 1–50 Hz, and bad channels were identified on the basis of being flat for > 5 s, and/or correlation to nearest neighbors < 0.8. Bad channels were removed and interpolated. EEG data were down-sampled to 512 Hz, datasets were re-referenced to the average reference, and adaptive mixture ICA (Palmer et al., 2008; Sejnowski, 1996) was performed. Resultant ICs were inspected, and classified into 7 categories (Brain, Eye, Muscle, Heart, Channel Noise, Line Noise, Other) using an automated component classifier (ICLabel v1.2.5) (Pion-Tonachini et al., 2019) that computes IC class probabilities for components. ICs with a brain classification below 0.7 were excluded from analysis. Remaining ICs were visually inspected for violation of the expected 1/f power spectral density, absence of a dipole projected across the scalp, and high-variance noise matching the incidence of heel strikes. ICs were back-projected onto continuous data. Target-locked epochs ranging from 100 ms preceding cue onset to 1200 ms after target stimulus onset were extracted relative to 100 ms pre-cue or 200 ms pre-target baselines. Trials were rejected on the basis of $+/- 250\mu V$ amplitude and 3 standard deviation threshold limits. Only trials responded to correctly 200–1000 ms after target onset were included in subsequent analyses. EEG preprocessing was performed using the EEGLAB toolbox (EEGLAB v14.1.2b) (Delorme and Makeig, 2004) and custom MATLAB scripts. After preprocessing an average of (mean per subject +/− 1SD) 200.77 +/− 24.21 sitting pure trials, 368.41 +/− 77.68 sitting mixed repeat trials, 94.45 +/− 22.39 sitting switch trials, 195.68 +/− 29.21 walking pure trials, 360.05 +/− 63.07 walking mixed repeat trials, and 92.86 +/− 19.35 walking switch trials remained for analysis.

2.7. ERP data analysis

Three (Diamond, 2013) preplanned time windows extending from 300 to 450 ms, 450 to 600 ms, and 600 to 750 ms post-cue onset were defined during the CTI to assess the centroparietal switch positivity and sustained frontal negativity (Karayanidis and Jamadar, 2014; Jamadar et al., 2015; Karayanidis et al., 2009, 2010, 2011; Gajewski et al., 2018; Jamadar et al., 2010). Midline electrodes were selected for analyses due to reliability of these sites for capturing these task-switching processes (Jamadar et al., 2015; Gajewski et al., 2018; Karayanidis et al., 2003; Nicholson et al., 2005, 2006; Gajewski and Falkenstein,

2011). Two (Miller and Cohen, 2001) time windows extending from 236 to 296 ms, and 300 to 500 ms were selected during the PTI to correspond to the expected post-target N2, and P3 respectively (Jamadar et al., 2015). The N2 interval was defined by encompassing (+ / − 30 ms) the average peak negative latency in the walking and sitting waveforms 200–400 ms after stimulus onset at electrodes Fz and Cz. The target-evoked P2 interval used in the post hoc analysis was defined following the same procedure to encompass the average peak positive latency 150–300 ms after stimulus onset. Cue-evoked P2 interval was defined to encompass (+ / − 30 ms) average peak positive latency at FPz 150–300 ms after cue onset. 3 × 2 × 3 repeated measures ANOVAs with factors trial type (pure, mixed repeat, or switch), physical condition (sitting or walking), and electrode (Fz, Cz or Pz) were performed at each of the preplanned and the post hoc target-P2 intervals. Mean amplitude over each interval was used as the dependent measure. A 3 × 2 repeated measures ANOVA with factors trial type and physical condition was performed at the post hoc cue-P2 interval. Mean amplitude at FPz was used as the dependent measure. A 2 × 3 repeated measures ANOVA, with factors block type (mixed or pure) and electrode (Fz, Cz, or Pz), compared walking-sitting difference waveforms during the PTI P3 interval (300–500 ms). Mean amplitude of the difference waveform during the time window was used as the dependent measure. When appropriate, the Greenhouse-Geisser correction was used to account for violation of the assumption of sphericity. Table 1 reports Greenhouse-Geisser corrected p-values. For post hoc analysis, the data were compared using Tukey's honest significant differences (HSD) test and effect sizes were measured using Cohen's d. Significance threshold was set at $a =$ 0.05.

2.8. Exploratory analysis–statistical cluster plots

To provide insight into the full breadth of this dataset's potential, statistical cluster plots (Molholm et al., 2002; Murray et al., 2002) were used to compare ERPs collected while seated to walking for each trial type. Pointwise two-tailed paired t-tests were applied across each sample point of the epoch window for each electrode. Subsequent points exceeding $a =$ 0.05 threshold for at least 11 consecutive sample points (> 20 ms) are considered significant (Guthrie and Buchwald, 1991). This technique controls Type I error rate across many tests while keeping the Type II error rate at a reasonably subdued level. This approach has been previously applied in exploratory analyses to permit a more comprehensive assessment of high-density EEG recordings (De Sanctis et al., 2014; Wylie et al., 2003).

3.   Results

3.1. Behavioral performance

Fig. 2 illustrates both individual and group level performance data for response accuracy (d'; top panel), and response times (bottom panel). A 2-way repeated measures ANOVA (trial type × physical condition) was performed comparing mean d' values across the six experimental conditions. Task performance depended on the type of trial (there was a main effect of trial type: F (2,42) = 8.66, $p =$ 0.0003). Participant d' values were higher on pure trials than either mixed repeat ($p =$ 0.0289) or switch trials ($p =$ 0.0001) suggesting there was a mixing cost to accuracy (Fig. 2 top panel). Contrary to expectations, there was no difference in d' when comparing mixed repeat to switch trials ($p =$ 0.2580) suggesting there

was no switch cost to accuracy during mixed blocks. There were also no differences in response times across pure, mixed repeat, or switch trials (main effect of trial type: F (2,42) = 1.97, p = 0.14), suggesting there was neither a mixing cost nor a switch cost to response time (Fig. 2 bottom panel).

Comparison of the seated and walking conditions revealed no main effect of physical condition on either d' values (F (1,21) = 0.19, p = 0.66) or response times (F (1,21) = 2.37, p = 0.13). The absence of behavioral differences as a function of physical condition (seated vs. walking) indicated that participants adapted well to the addition of simultaneous walking for both pure blocks and mixed blocks, with no evident consequences for task performance.

3.2.   Gait kinematics

Fig. 3 illustrates progressive changes to gait kinematics as cognitive-motor load increased. 1-way repeated measures ANOVA (block type) showed gait characteristics depended on whether a participant was only walking, or engaged in a pure or mixed block. There was a main effect of block type for stride length (F (2,40) = 26.54; $p < 0.0001$, $\eta_p^2 = 0.5703$), stride length variability (F (2,40) = 6.33; $p = 0.0113$, $\eta_p^2 = 0.2404$), stride time (F (2,40) = 5.50; $p = 0.0088$, $\eta_p^2 = 0.2156$), and stride time variability (F (2,40) = 6.48; $p = 0.0088$, $\eta_p^2 = 0.2448$). Post-hoc tests (Tukey HSD) comparing mixed and walking only blocks showed lower stride length variability ($p = 0.0006$, $d = 0.7275$) and lower stride time variability ($p = 0.0005$, $d = 0.6326$) during mixed blocks, but no differences in stride length or stride time. Despite covering similar distances with strides of similar duration, gait pattern consistency improved when participants performed the most challenging block of the cognitive task, as compared to focusing solely on walking. Narrower and higher peaked group distributions for mixed blocks in Fig. 3 B and 3 D illustrate the improved gait consistency.

Gait in pure blocks did not have detectable differences in variability, but consisted of shorter and quicker strides. There were no differences in stride length variability when comparing pure blocks to walking only ($p = 0.48$, $d = 0.2546$) or mixed blocks ($p = 0.06$, $d = 0.3646$), and no differences in stride time variability when comparing pure blocks to walking only ($p = 0.14$, $d = 0.4077$) and mixed blocks ($p = 0.55$, $d = 0.1732$). Stride lengths were shorter in pure blocks compared to both walking only ($p < 0.0001$, $d = 0.3881$) and mixed blocks ($p < 0.0001$, $d = 0.3405$). Stride times were also shorter in pure blocks than in walking only ($p = 0.0345$, $d = 0.1796$) and mixed blocks ($p = 0.0275$, $d = 0.1604$). This suggests participants may have reduced duration of single support time through quicker and more frequent strides covering less distance.

3.3.   Electrophysiology overview and description

A key motivation to investigate cognitive control during walking stems from the hypothesis that walking can interfere with these processes. This leads to the prediction that differences in these processes will be revealed by examination of the ERPs during the cue-target interval (CTI) and post-target interval (PTI). The grand average traces in Fig. 4 for each condition were aligned at the onset of the imperative "target " (Gabor patch) stimulus (0 ms, vertical black line). Baselines for the cue-evoked (Fig. 4 A) and target-evoked (Fig. 4 B) neural responses were calculated over the 100 ms interval preceding the onset of the cue (− 750

ms, vertical red line) and 200 ms interval preceding the onset of the target stimulus (0 ms, vertical black line) respectively. Visual inspection of these ERPs revealed differential neurophysiological responses related to task conditions during both the cue-evoked and target-evoked periods.

Waveforms over frontal scalp (Fz) showed a clear negativity peaking at ~150 ms post-cue, followed by a positivity peaking ~50 ms later. There was a clear difference in the amplitude of the positive potential during switch trials (light and dark red traces) compared to either pure (light and dark green) or mixed repeat (yellow and orange) trials. Additional positive-going components, most prominent on switch trials, appeared later in the CTI over central scalp (Cz, ~250–450 ms post cue), and later still over parietal scalp (Pz, ~450 ms post-cue).

The subsequent target stimulus evoked a second series of pronounced neurophysiological responses. Over frontal scalp (Fz) there was a positive peak ~200 ms post target presentation. Following this, traces clearly separated based on whether the task was performed while seated or walking at ~250 ms post-target, until ~400 ms. A subsequent separation based on task occurred in the 450–600 ms post-target window (pure trials were associated with a smaller and later peaking positivity compared to mixed repeat and switch trials). These differences in the target-evoked response were also present at Cz and Pz locations, albeit with different timing and amplitudes.

To disentangle potentially overlapping proactive and reactive processes, measurements across intervals within the CTI and PTI were collected relative to separate pre-cue (Fig. 4 A) and pre-target (Fig. 4 B) baselines (Gajewski and Falkenstein, 2011; Gajewski et al., 2010 b; Gajewski and Falkenstein, 2015). Mean amplitude was measured at three midline electrodes (Fz, Cz, and Pz) across each preplanned interval in Fig. 4 (gray bands). The scatter plots and probability density functions in Fig. 5 show individual participant measurements and group variance respectively for each experimental condition at each preplanned interval (rows) and electrode (columns).

3.4. Walking alters neural activity during proactive control

The 'centroparietal positivity' associated with proactive control during task-switching experiments has been shown to begin around 300 ms after cue onset and to persist through target presentation (Karayanidis et al., 2011 b). Due to the protracted duration of this response, it was divided into three consecutive 150 ms intervals (gray bands in Fig. 4 A). A 3-way repeated measures ANOVA (trial type $\times$ physical condition $\times$ electrode) was performed comparing neural responses in each interval (ANOVA details are presented in Table 1; individual participant measurements used for ANOVA inputs are presented in Fig. 5). In the earliest interval (300–450 ms), the amplitude of the centroparietal positivity depended on the type of trial (there was a main effect of trial type ($F_{(2,42)} = 13.43$, $p = 0.0005$) as shown in Column 1, Row 1 of Table 1). Post-hoc Tukey's HSD showed a larger ERP response in this time window during switch trials compared to pure trials ($p = 0.0028$, $d = 0.6492$) and also compared to mixed repeat trials ($p = 0.0017$, $d = 0.4595$). There was no detectable difference between mixed repeat and pure trials ($p = 0.1163$, $d = 0.2492$). The larger amplitudes evoked by switch trials can also be seen by comparing the probability density functions in row 1 of Fig. 5. There was no main effect of physical condition (walking

compared to seated responses), as shown in column 1, row 2 of Table 1 (F (1,21) = 2.46, p = 0.1319), indicating a consistent centroparietal positivity in this early post-cue time window that did not depend on whether participants were walking or sitting.

In the subsequent 150 ms interval, extending from 450 to 600 ms after cue presentation (second gray band in Fig. 3 A), the ERP waveforms over parietal scalp (Pz) continued to show an increased positivity. The response evoked during switch trials remained the largest (light and dark red traces in Fig. 4 A; row 2 in Fig. 5). The ANOVA results in Table 1 show a main effect of trial type (row 1, column 2). During this interval there was also a main effect of electrode (row 3, column 2) consistent with the more posterior distribution of the positivity seen in Fig. 4 A, and reflected in the larger positive amplitude measurements at Pz (Fig. 5, row 2, column 3). A trial type by electrode interaction was also present (F (4,84) = 15.48, p < 0.0001) and post-hoc Tukey HSD tests showed that activity observed over central scalp (Cz) during switch trials was greater than that during mixed repeat trials (p = 0.0019, d = 0.6983) and also during pure trials (p < 0.0001, d = 1.1834). Similar results were seen at electrode Pz with switch-related activity greater than during mixed repeat trials (p < 0.0001, d = 0.8339) and greater than during pure trials (p < 0.0001, d = 1.2620). Unlike the activity recorded during the earliest 150 ms interval, the response evoked by mixed repeat trials was larger than that of pure trials at both Cz (p < 0.0001, d = 0.6213) and at Pz (p = 0.0043, d = 0.5252). There was no main effect of physical condition during this second 150 ms epoch. This suggests that the different demands on proactive control mechanisms of pure, mixed repeat, and switch trials were not altered by the addition of walking in this interval.

During the final 150 ms interval immediately preceding presentation of the target stimuli, the first indication of neurophysiologic changes in proactive control due to walking appeared in the ERPs (Fig. 4 A right-most, gray band). There was a "sustained frontal negativity ", previously identified as a marker of proactive control (Gajewski et al., 2018; Astle et al., 2008), that was largest during switch trials compared to pure trials at site Fz (p = 0.0199, d = 0.6136) and at the same site when comparing switch and mixed repeat trials (p = 0.0398, d = 0.4085). This frontal negativity was larger when participants performed the task walking compared to sitting, indicating walking altered neural activity during this proactive control process (F (2,42) = 5.87, p = 0.0167; row 6, column 3 in Table 1). This walking-sitting difference was reflected in a negative shift in the probability density functions of mean amplitude at Fz while walking relative to sitting (Fig. 5 row 3, column 1). The post-hoc test comparing sitting and walking at electrode Fz in this interval also showed a difference in ERP amplitude (p = 0.0088, d = 0.2535). The frontal negativity was largest during switch trials, consistent with observations of other task-switching studies (Astle et al., 2008). The walking-dependent changes to the frontal neural response suggested that the trial-dependent late frontal proactive processes were altered by the addition of a motor load.

3.5. Walking alters neural activity during reactive control

Reactive control encompasses a set of processes executed "on the fly " as needed following an imperative stimulus. Little is known about how walking during task execution affects reactive control processes. To assess target-evoked reactive control, two time windows were selected corresponding to the N2 component, extending from 236 ms to 296 ms (Fig. 4 B;

left-most gray band), and to the P3 component of the ERP, extending from 300 ms to 500 ms (Fig. 4 B; right-most gray band). Mean amplitude measurements from these intervals are presented in rows 4 and 5 of Fig. 5 respectively. See Methods for details on selection of time windows for these analyses.

Neural processes reflected by the fronto-centrally recorded N2 (~230 ms post target) differed by trial-type ($p < 0.0001$), electrode location ($p = 0.0280$), and physical condition (walking vs. sitting; $p = 0.0101$) (Table 1). Interactions of trial-type X electrode ($p = 0.0082$), and physical condition X electrode ($p = 0.0167$) were also observed.

The neural response was altered over frontal and central scalp during walking, and may reflect a neurophysiologic representation of cognitive-motor interference. Post-hoc tests (Tukey's HSD) showed less negative (smaller) N2 components during walking both at Fz ($p < 0.0001$, $d = 0.4255$) and at Cz ($p = 0.0014$, $d = 0.2756$). The upward shifts in the probability density functions of amplitude while walking reflect the diminished negativity (Fig. 5, row 4, columns 1 and 2). Over central electrodes, switch trials produced larger (more negative) N2 component amplitudes than did mixed repeat trials ($p = 0.0007$, $d = 0.2898$) or pure trials ($p = 0.0024$, $d = 0.5046$). There was no difference across trial types at Fz ($p = 0.9885$, $d = 0.0218$). These trial-dependent changes suggest a progressive increase in N2 amplitude across pure, mixed repeat, and switch trials related to the serial increase in difficulty occurring across these trial types. The relatively higher interference of switch trials was therefore associated with a larger N2 than either mixed repeat, or pure trials.

In the second pre-defined reactive control interval that corresponds to the P3 ERP component (300–500 ms after stimulus presentation) there were clear differences in responses that depended on trial type and also on walking. These can be seen in Fig. 4 B as the ERP responses (for example) at electrode Pz differ as a function of presumed load with walking-switch trials (dark red) having the smallest P3, sitting-switch trials (light red) slightly larger, walking-mixed repeat (orange) larger still, et cetera. The trial and walking-dependent shifts in the probability density functions of amplitude indicate these differences reflect consistent changes to the neural responses of the participants, as opposed to an effect driven by outliers (Fig. 5, row 5). The ANOVA results (Table 1) showed interaction terms for trial type X electrode ($p < 0.0001$), physical condition X electrode ($p < 0.0001$), and the three way interaction of physical condition X trial type X electrode ($p = 0.0273$). Trial-dependent differences in the neural responses occurred when either seated or walking, but the difference was larger when participants were walking. The larger trial-dependent changes identified during walking during the P3 interval suggests that additional exertion further amplifies the dissociation of reactive control processes.

3.6. Walking-Dependent changes to control processes are larger when cognitive load is higher

The changes to cued task-switching ERPs occurring during walking are hypothesized to stem from the response of underlying neural processes to increased demands upon shared resources. This hypothesis predicts that walking-dependent changes to control processes will be greater in circumstances when overall demands are higher, and conversely, lesser when demands are lower. In the current experiment, higher task demands occurred during mixed

blocks. To compare walking-dependent changes across instances of higher and lower task demands, the difference between ERPs recorded while walking and sitting (walking minus sitting) for pure (green), mixed repeat (orange) and switch (red) trials are shown in Fig. 6. Walking-sitting difference waveforms for the CTI and PTI are displayed in Fig. 6 A and 5 B, respectively. Topographical maps of walking-sitting mean amplitude differences during the preplanned CTI and PTI intervals are displayed in a matrix beneath the difference waveforms in Fig. 6. This approach separates task-dependent responses to each trial type, isolating distinct task-independent features attributable to the physical condition of the participant. To compare differences in walking-dependent changes related to whether a trial was executed with, or without attention switching requirements, a two-way repeated measures ANOVA was performed with factors block type (mixed and pure) and electrode (Fz, Cz, Pz). On the basis of the trial and walking-dependent differences during the P3 interval, mean amplitude of the difference waveform during the 300–500 ms PTI interval was the dependent measure.

As noted previously, neurophysiologic changes in the second pre-defined reactive control interval (300–500 ms) depended on the trial type, the EEG electrode location, and the physical condition (walking or sitting). Differences in the neural response due to walking were larger during mixed block trial types (mixed repeat and switch) and may represent the effects of increased demand on cognitive motor interactions. This can be seen in Fig. 6 B as the difference waveforms at Fz and Pz appear to differ based on whether the trials were performed in a block with switching requirements. Topographical maps of walking-sitting differences during this interval showed a broad positivity over fronto-central scalp and negativity over parietal scalp that were more pronounced during mixed repeat and switch trials (Fig. 6, column 5 of topographical map matrix). The ANOVA results show an interaction term for block type X electrode (F (2,42) = 8.571, $p = 0.0030$, $\eta_p^2 = 0.2898$). Post-hoc tests (Tukey's HSD) showed larger differences due to walking during mixed block trial types at Fz ($p = 0.0373$, $d = 0.5186$) and Pz ($p = 0.0023$, $d = 0.6091$). The larger walking-dependent changes identified on mixed block trials during the P3 interval suggests that increasing task-related demands on reactive control processes amplifies modulation of the neural response due to walking.

3.7. Exploratory analysis–statistical cluster plots (SCPs)

Testing *a priori* hypotheses at few electrodes risks overlooking unanticipated effects. Therefore, an exploratory analysis was conducted across the entire data matrix as a means of hypothesis generation for further study. A statistical cluster plot (SCPs; see methods (De Sanctis et al., 2014; Molholm et al., 2002; Murray et al., 2002; Foxe and Simpson, 2002)) was generated for each trial type to compare neural responses across physical conditions (Fig. 7). These intensity plots show the results of t-tests comparing the seated and walking conditions; the x-axis is time, the y-axis is electrode location, and the z-axis is *t*-test result.

SCPs provide insight into differences between trial types in the timing, duration, and distribution of previously identified walking-dependent changes. Clusters of walking-dependent changes to late frontal and parietal proactive processes emerged during each trial type ~200 ms prior to the target stimulus. These differences subsided earlier during

pure trials, such that an interval without neural changes due to walking preceded target stimulus onset. Conversely, neurophysiological changes due to walking continued to impact late proactive processes of mixed repeat and switch trials, until target stimulus onset. These results may represent reconciliation of the effects of walking upon proactive processes during less demanding trial types, and a persistent interference during more demanding trial types. The SCPs also exposed putative walking-dependent changes to early frontopolar proactive processes (~100–200 ms after cue onset) of switch trials that were absent on other trial types. An additional 3 (trial type) × 2 (physical condition) ANOVA was performed to assess the putative changes at FPz (see methods for definition of interval). ANOVA results showed a main effect of trial type (F (2,42) = 13.09, $p = 0.0002$, $\eta_p^2 = 0.3840$), but no effect of physical condition.

The duration of previously identified walking-dependent changes to frontal and parietal reactive processes was also shorter during pure trials, and longer during mixed repeat and switch trials. Again, longer duration changes due to walking on mixed block trials may represent a more persistent interference by walking upon reactive processes. Also, the SCPs suggested that walking-dependent changes at the N2 and P3 intervals may be continuous. Novel clusters of putative walking-dependent changes to early (150–200 ms) and later (600–800 ms) reactive processes were also identified over frontopolar, frontal, parietal, and occipital scalp regions. These clusters were more prominent in SCPs of mixed block trial types, suggesting walking-dependent changes to the early and later reactive processes may also depend on the demands of a given trial type. A 3 (trial type) × 2 (physical condition) × 3 (electrode; Fz, Cz, Pz) ANOVA was performed to address the novel early clusters roughly corresponding to a P2 (see methods for definition of interval). The ANOVA results showed a three-way interaction of trial type X physical condition X electrode (F (4,84) = 3.73, $p = 0.0296$, $\eta_p^2 = 0.1507$). Post-hoc Tukey HSD tests showed that walking increased the amplitude of the positivity at Fz on mixed repeat ($p < 0.0001$, $d = 0.3728$) and switch ($p = 0.0351$, $d = 0.3250$), but not pure trials ($p = 0.8878$, $d = 0.1106$). A similar increase in amplitude occurred at Cz also on mixed repeat ($p = 0.0013$, $d = 0.4388$) and switch ($p = 0.0351$, $d = 0.3555$), but not pure trials ($p = 0.0798$, $d = 0.2885$). Again, these results suggest increasing task-related demands on reactive control processes amplifies modulation of the neural response due to walking.

4. Discussion

A cued task-switching design was used to study the effect of walking on proactive and reactive cognitive control processes. The task dissociated the cognitive processes occurring when information about task rules was first provided by a cue (proactive control in the Cue-Target Interval) from processes linked to choosing the correct visual target (reactive control in the Post Target Interval). The simplest form of the task occurred during blocks of trials in which only one type of visual discrimination was required (pure blocks). Difficulty increased when participants were required to alternate between two types of visual discrimination (orientation or spatial frequency) in the same block. These mixed blocks required holding two sets of task rules at the ready, and waiting for cue-based information about which task to implement. During mixed blocks, a trial might repeat the rules of the previous trial or switch to the rules of the other discrimination task. Switching task rules

required suppression of the current task and implementation of the alternate. In each of these subsets of trials, interference from the sensory-motor requirements of walking was hypothesized to provide additional load on available resources. Consequently, there were six levels of task difficulty, scaling from the simplest (sitting pure trials) to the most demanding (walking switch trials). Objective EEG measures were used to assess the relative increase in cognitive load caused by the addition of walking, and the different impact walking had on proactive and reactive cognitive control processes. Positional motion capture data were used to assess the effect of increasing cognitive load on gait kinematic measures.

4.1. Proactive control during walking

During the CTI, the earliest task-specific differences in evoked responses were seen frontally during the P2 timeframe. Early frontal dissociation of cue-evoked activity between switch and repeat trials has been reported (Astle et al., 2008; Lavric et al., 2008; Tarantino et al., 2016), and may indicate sensitivity to switch cue salience, facilitating task preparation. Wong and colleagues suggest this early positivity reflects a putative frontal generator involved in rapid cue-evoked dissociation of trial types (Wong et al., 2018). The frontal early positivity was present in the data, but statistical analysis did not reveal walking-related modulation at the regions tested. However, SCP analysis identified a possible frontopolar walking-related modulation to the early positivity.

The amplitude of the late sustained frontal negativity increased during walking. Sustained frontal negativity amplitude increases as a function of effort and task difficulty (Falkenstein et al., 2003; Kray et al., 2005; West, 2004), suggesting simultaneous walking renders task preparation more difficult, requiring more effortful proactive processing. Amplitude of the sustained frontal negativity has also been correlated with higher task performance (Gajewski et al., 2010 a). Therefore, amplification of sustained frontal negativity during walking likely indicates the additional recruitment of fronto-executive control when task switching and walking co-occur to successfully maintain performance.

4.2. Reactive control during walking

The target-evoked N2 is a fronto-central ERP component thought to be generated by contributions from the ACC and SMA that is associated with conflict processing in service of response selection (Jamadar et al., 2015; Irlbacher et al., 2014; Iannaccone et al., 2015). The amplitude of the N2 has been shown to be smallest on pure trials, larger on mixed repeat trials, and largest overall on switch trials, reflecting the progressive interference caused by maintaining multiple sets of task rules at the ready and by replacing one set of rules with another (Jamadar et al., 2015) (b). Increased target-driven interference stemming from properties of the target stimulus or stimulus-response mapping has been shown to further increase the amplitude of the N2. In the data shown here, reduction in N2 amplitude while walking may be surprising considering the addition of walking-associated sensorimotor processes could be another source of cognitive interference. DeSanctis and colleagues proposed that walking-dependent reductions in N2 amplitude indicated a shift away from early and automatic processes towards a later and more effortful mode of cognitive processing reflected in subsequent changes to the neural response. Reconciling additional cognitive load stemming from walking may exceed the capacity of the neural

processes engaged to resolve changes in cue or target-driven interference. Resolving CMI may instead require mustering of additional frontal executive processes, an interpretation which aligns well with the hemodynamic changes observed during cognitive motor tasks (Holtzer et al., 2011; Al-Yahya et al., 2016).

One established measure of cognitive loading is the parietal P3 component of the ERP. The amplitude of the P3 has been interpreted as being related to the intensity of processing (Donchin et al., 1986). A reciprocal relationship between P3 amplitude and task complexity has been demonstrated in both single and dual-task designs (Kok, 2001). In single task experiments, increasing working memory load (Kramer et al., 1986) and manipulation of task difficulty (Kok, 1986) reduced P3 amplitude. Dual-task designs produced smaller P3 amplitudes compared to their single-task counterparts. One account of the reduction in P3 amplitude proposed that depletion of perceptual-cognitive resources occurs as task demands mount, resulting in correspondingly fewer resources available for P3-related processes (Kok, 2001, 1997; Kramer et al., 1986; Strayer and Kramer, 1990). This interpretation aligns well with the reciprocal trade-offs between P3 amplitudes observed to occur as experimental demands or priorities were shifted between the dual tasks (Strayer and Kramer, 1990; Wickens et al., 1983; Hoffman et al., 1985). The intent of dual-task designs is in part to approach or to reach full utilization of processing capacity. Electrophysiological trade-offs in P3 amplitudes can thus be viewed as re-allocation of resources towards the prioritized (or more demanding) task, at cost to the other, secondary task. Here, the demands of walking were added to a task-switching design to systematically increase difficulty. This pairing comprises changes to multiple determinants of P3 amplitude: task-related working memory, task difficulty, and addition of a second, simultaneous task.

As expected, the clearest measure of relative cognitive load can be seen at the parietal locus (Pz) during the P3 epoch following presentation of the target (see Fig. 4 B). During pure blocks, the addition of walking had no effect on component amplitude. However, during mixed repeat trials, component amplitude was reduced compared to pure block trials and the addition of walking further decreased the amplitude of the P3. The more difficult switch trials produced still more reduction in component amplitude and the addition of walking to switch trials produced a larger reduction than was produced during mixed repeat trials. As indicated by reduction of parietal P3 amplitude, the effect of walking on the neural response became more pronounced as concomitant task-related effects on cognitive load also increased. This may reflect a progressive effect of walking on the allocation of cognitive resources. Thus, if the overall task is simple enough and taxes available resources very little, then the addition of walking has little or no observable effect. However, as the requirements of the task consume more resources and, perhaps, additional circuitry is recruited, walking produces an ever-greater drain on these same resources, at least as indicated by the amplitude of the parietal P3. This neurophysiological evidence for walking affecting task-related allocation of attentional resources aligns well with observations that individuals with reduced attentional capacity (mild cognitive impairment and Alzheimer's disease patients) exhibit the most pronounced performance deficits in cognitive-motor tasks (Al-Yahya et al., 2011; Montero-Odasso et al., 2017; De Sanctis et al., 2020).

4.3. Cognitive control effects on gait

Gait measures were less variable as cognitive demands increased. The most stable gait pattern (lowest stride variability) was observed during the most demanding block type: mixed blocks. Proactive and reactive control processes which mediate reconfiguration of gait permit anticipatory and responsive adaptation to loss of balance, environmental changes, or hazards (Wagner et al., 2019, 2016; Sipp et al., 2013; Nordin et al., 2019; Haefeli et al., 2011; Potocanac et al., 2015) in part through diminished automaticity and at a cost of increased variability (Hausdroff, 2005; Newell, 1993). Orienting attention towards gait motor processes increases susceptibility to endogenous or exogenous noise (Hamacher et al., 2019 b; Beilock and Gray, 2012; Beilock et al., 2002), counterproductively degrading gait stability when immediate adaptations are not required. In the dual task framework of cognitive-motor interactions, shifts in attention away from motor processes reduces susceptibility to noise, and restores automaticity so long as cross-modal resource competition does not exceed capacity limits (Lövdén et al., 2008) (a). In the context of the dual-process frame work, reduced stride variability during mixed blocks can be interpreted as diversion of attentional resources to proactive and reactive control processes of the cognitive task, without exceeding capacity limitations beyond which stride and task performance would deteriorate. Stabilization of gait during mixed blocks and the absence of walking-related performance costs indicate that participants either adapted to, or were facilitated by the cognitive-motor load in the current experiment.

Gait during walking pure blocks consisted of shorter and quicker strides. However, these blocks disproportionately represent the earliest walking intervals completed by participants, as pure blocks necessarily preceded mixing of task instructions. Therefore gait changes during pure blocks may reflect reconfiguration of cognitive control over motor processes confounded with ongoing adaptation to treadmill walking (Meyer et al., 2019).

4.4. Summary and future directions

While walking-related effects were observed to occur during ERP indices of both proactive and reactive control, the differential walking-related effects were larger, more enduring, and more broadly distributed across scalp regions at intervals corresponding to reactive cognitive control processes. These results were counter to our expectations that proactive processes would be sensitive to scarcer resource availability during walking. This observation suggests that reactive control mechanisms are in fact more susceptible to cognitive-motor interference, at least in a cohort of young healthy adults. Larger effects on reactive versus proactive control processes on attentional capture and reorientation (Braver, 2012) have been shown. The detection-response mechanisms of reactive control, within the context of urgently shifting cognitive demands, may be more sensitive to perturbation from concurrent sensory-motor activity than proactive control processes. Conversely, the sustained and anticipatory nature of proactive processes may render these processes comparatively resilient to the effects of walking in an unexpected manner. From a technical perspective, it is worth noting that recording slow potentials is not nearly as vulnerable to walking as one might have predicted. The sustained proactive processes over frontal and parietal scalp present in the data recorded while seated were recapitulated in the data recorded while walking.

No aspects of the kinematic, behavioral, or the neurophysiological data suggested an overt shift to a reactive style of processing. It may be the case that the difficulty of the task paradigm failed to push participants beyond a 'tipping point' into predominantly reactive control. Further increasing the overall demand of the task may yet identify a point at which behavioral deficits or neurophysiological changes indicating less successful preparation appear. This paradigm affords several options for increasing overall difficulty, through modification of cognitive task parameters, or simply increasing the demands of walking (e.g. variable speed demands). We hypothesize that a shift to a predominantly reactive control strategy depends on overall demand exceeding a 'tipping point' beyond which resources normally directed to proactive processes are instead occupied by prioritization of ambulation, motor error correction, and hazard avoidance. This 'tipping point' may vary across individuals depending on baseline reserves of cognitive resources, and the degree to which walking is prioritized over the cognitive task.

Use of a treadmill walking affords rigid control over parameters of the cognitive-motor load and a predictably consistent walking surface, but requires participants to match the treadmill's pace in a manner which may reduce variation in gait characteristics typical of natural walking patterns (Sloot et al., 2014). An alternative is over-ground walking (Reiser et al., 2019), which would improve ecological validity of this experiment. However, a self-paced approach that does not require participants to match their pace to a moving surface may result in inconsistent cognitive-motor load throughout a walking interval, and the experiment. Ultimately, both approaches possess pitfalls, and each provide insight into how cognitive-motor interactions occur in real-world settings. However, direct comparison of these studies should done with caution, as cognitive control of gait is different during over-ground and treadmill walking (Wrightson and Smeeton, 2017; Bayot et al., 2018).

Walking-dependent changes to the neural response occurred despite participants generally maintaining task performance during walking, and stride variability decreasing. The resiliency of participants' performance measures to a simultaneous motor load suggests they successfully adapted to the altered task parameters. As such, walking-dependent changes to the neural response may reveal the underlying adaptive measures that maintain behavioral performance in the face of increasing task demands. The progressive changes in neurophysiology as task demands increase are unlikely to proceed indefinitely. If task demands continued to increase it is expected at some point that instead of covert changes in neural processing, overt changes in behavior and gait would be observed. In addition, if there were participants who for whatever reason were less flexible in their ability to alter neural activity to compensate for task load, they would be expected to reach this 'saturation point' more quickly. Using a systematically graded cognitive task coupled with walking has the potential to uncover latent deficits in neural adaptability and flexibility before overt decay of behaviors can be detected.

Earlier task-switching experiments have shown that younger adults tend to use proactive control, whereas healthy older adults rely more heavily on reactive control mechanisms (Braver et al., 2009; Paxton et al., 2008; Kopp et al., 2014; Jimura and Braver, 2009). The extent of the changes to reactive control that occurred during walking suggests that this may be a useful paradigm for studying older adults, and identifying age-related differences in the

effect of walking upon control processes. Additionally, the increased effects of walking as task-dependent load increases may provide an objective measure of cognitive ability in older adults. For instance, those who have some underlying (or undiagnosed) cognitive decline are more likely to show walking-linked changes in ERPs during trial types that are easier than older adults who are less impaired.

The addition of walking to ongoing tests of executive function is important as a move toward more ecologically relevant assessment of cognitive ability. It is also a tool to systematically manipulate cognitive load to uncover covert decline, and extend understanding of the interactions between sensory, motor, and cognitive processing.

Acknowledgments

Data sharing statement

Data and custom code from this study will be made available through a public repository (e.g. Figshare) upon publication of this paper, and the authors will work with the editorial office during production to incorporate appropriate links.

Abbreviations:

CMI	cognitive motor interference
EEG	electroencephalography
ERP	event-related potential
MoBI	Mobile Brain-Body Imaging
CTI	cue-target interval
PTI	post-target interval
ACC	anterior cingulate cortex
PPC	posterior parietal cortex
DLPFC	dorsolateral prefrontal cortex

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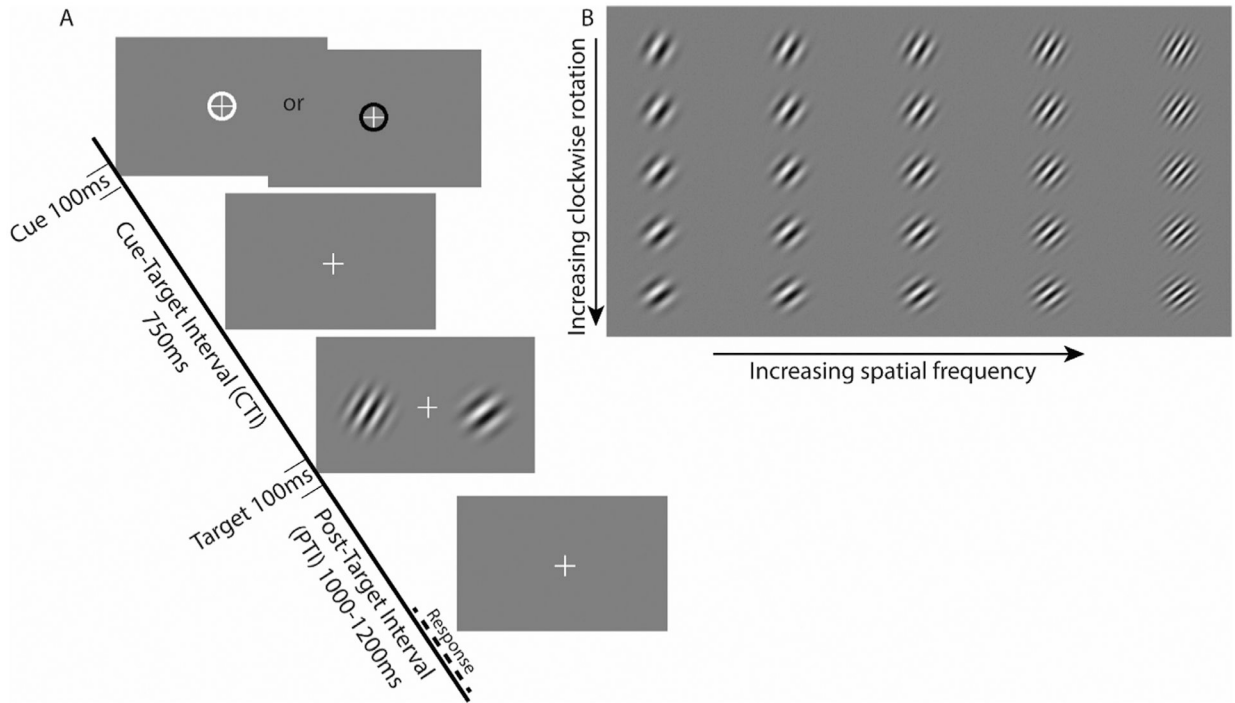
Fig. 1.
Task-Switching Design (A). During "pure " blocks a white or black annulus around the fixation cross was presented for 100 ms. During "mixed " blocks white and black annuli were presented with 3, 4, or 5 identical trials presented before switching cue. A 750 ms delay after cue presentation was followed by a 100 ms presentation of the target image (a pair of Gabor patches selected at random from the array of possible targets (B). Response times varied but occurred within the 1000–1200 ms post-target interval. Responses consisted of pushing left or right Nintendo Joy-Cons [™] buttons to indicate selection. Cues instruct participant to perform either the spatial frequency discrimination task or the angle discrimination task.
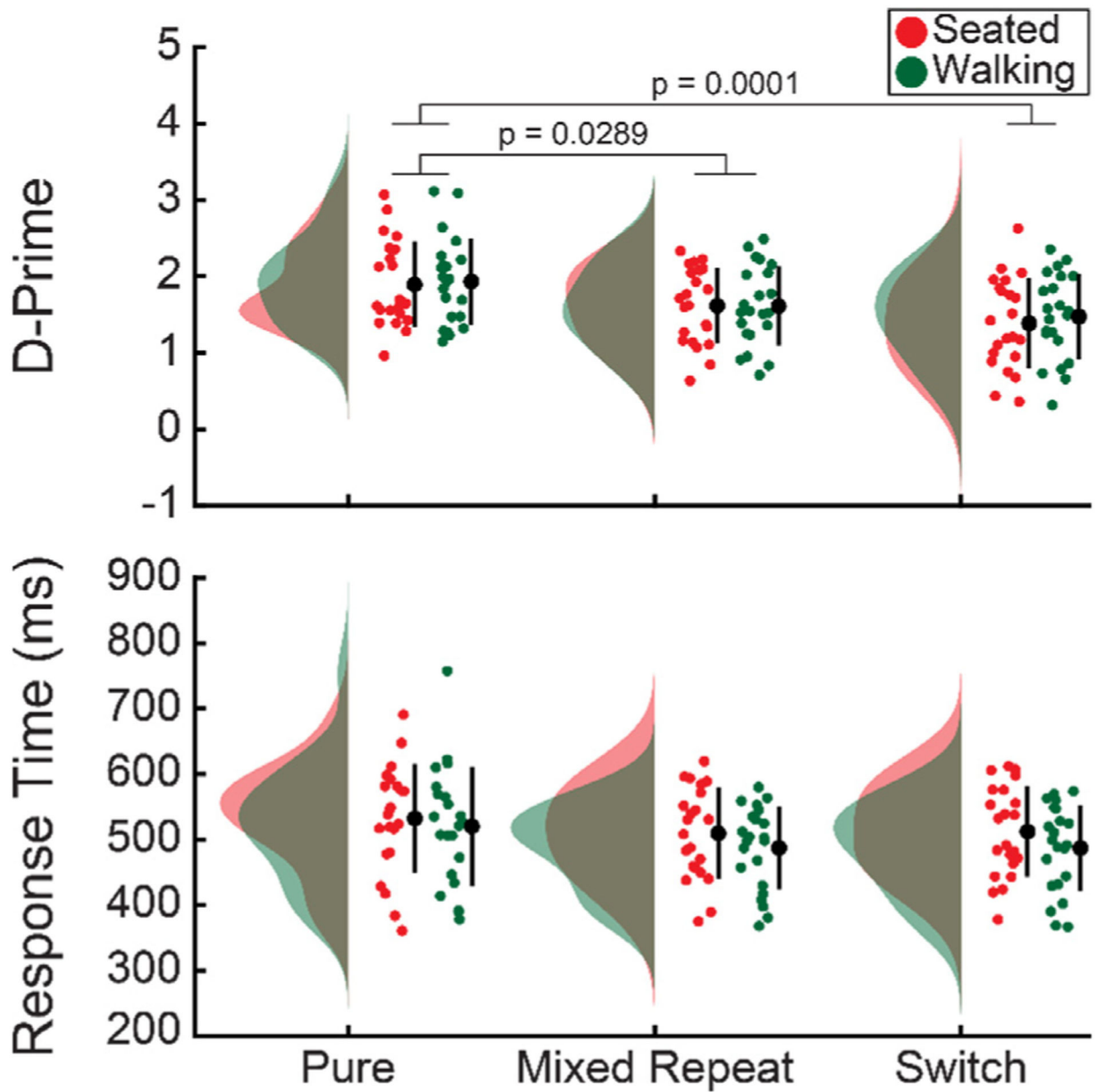
Fig. 2.
Task performance data for pure, mixed repeat, and switch trials conducted while seated (red) or walking (green). Group distribution curves and individual participant values are illustrated for each condition. Black dots and whiskers indicate group means +/− 1SD. Displayed p-values were produced using Tukey's HSD. Top Panel: Accuracy levels expressed as d-prime values. Colored dots to the right of distribution curves indicate individual participant d-prime values. Bottom Panel: RT data. Colored dots to the right of distribution curves correspond to individual participant mean RTs (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).
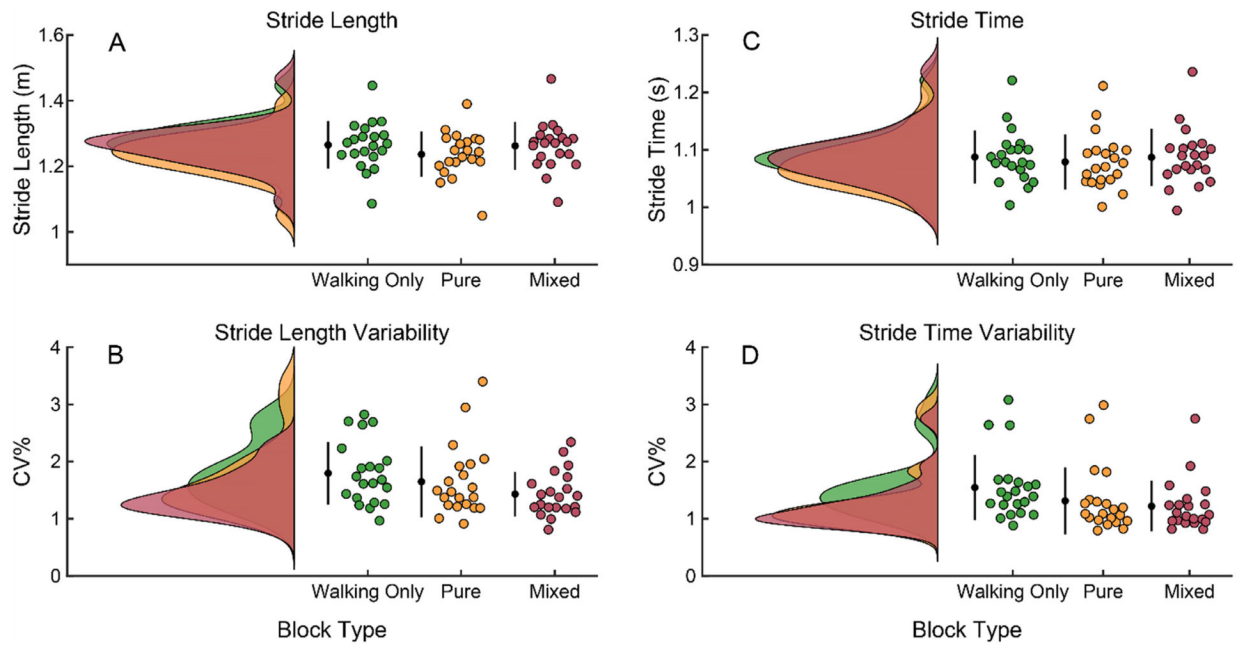
Fig. 3.

Kinematic gait measurements. Colored dots show individual participant means during walking only, walking during pure blocks and walking during mixed blocks. Group distributions are shown for stride length (A), stride length variability (coefficient of variation) (B), stride time (C) and stride time variability (coefficient of variation) (D) across each block type. Black dots and whiskers indicate group means +/− 1SD.
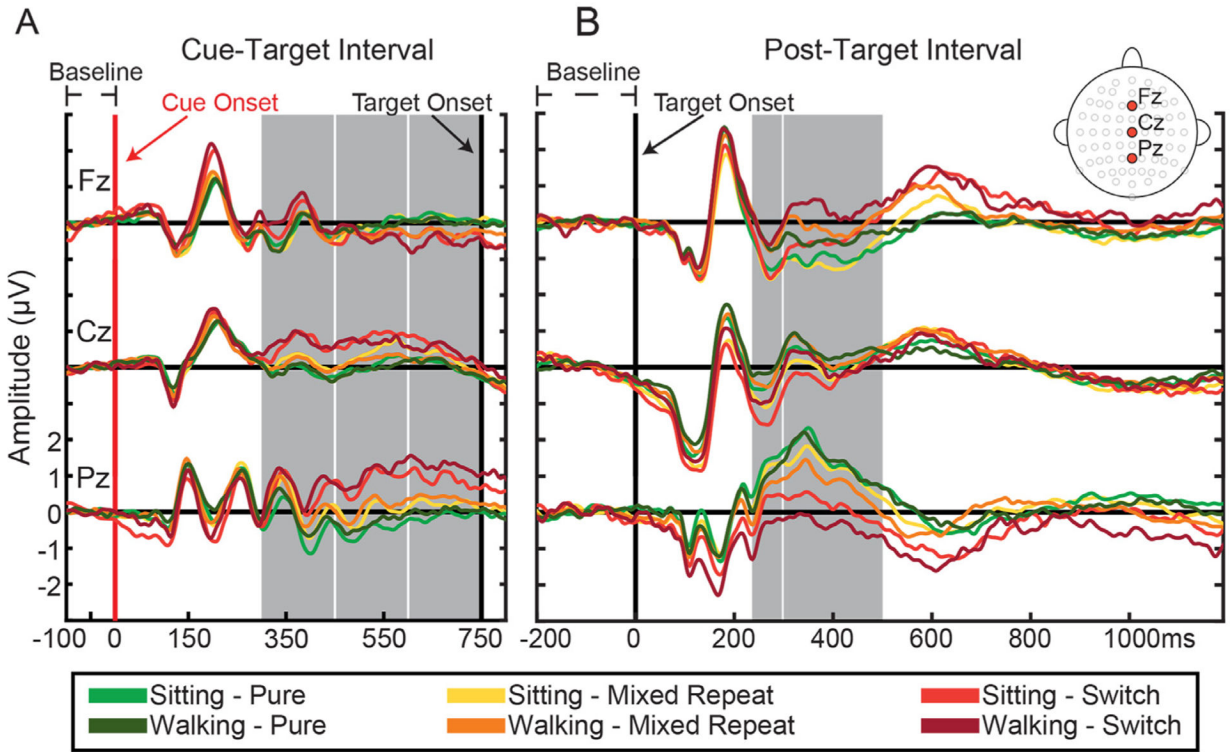
Fig. 4.
ERPs separated into Cue-target (A) and Post-target intervals (B). Shaded regions illustrate temporal epochs based on pre-planned comparisons. The 3 preplanned cue-target intervals (− 450 to − 300 ms; − 300 to − 150 ms; −150 to 0 ms) and 2 preplanned post-target intervals (236 to 296 ms; 300 to 500 ms) are indicated by gray bands. The scalp map in the upper right corner of the figure displays electrode locations for displayed traces (anterior to posterior): Fz, Cz, and Pz. Vertical red and black lines indicate cue and target stimulus onset respectively.
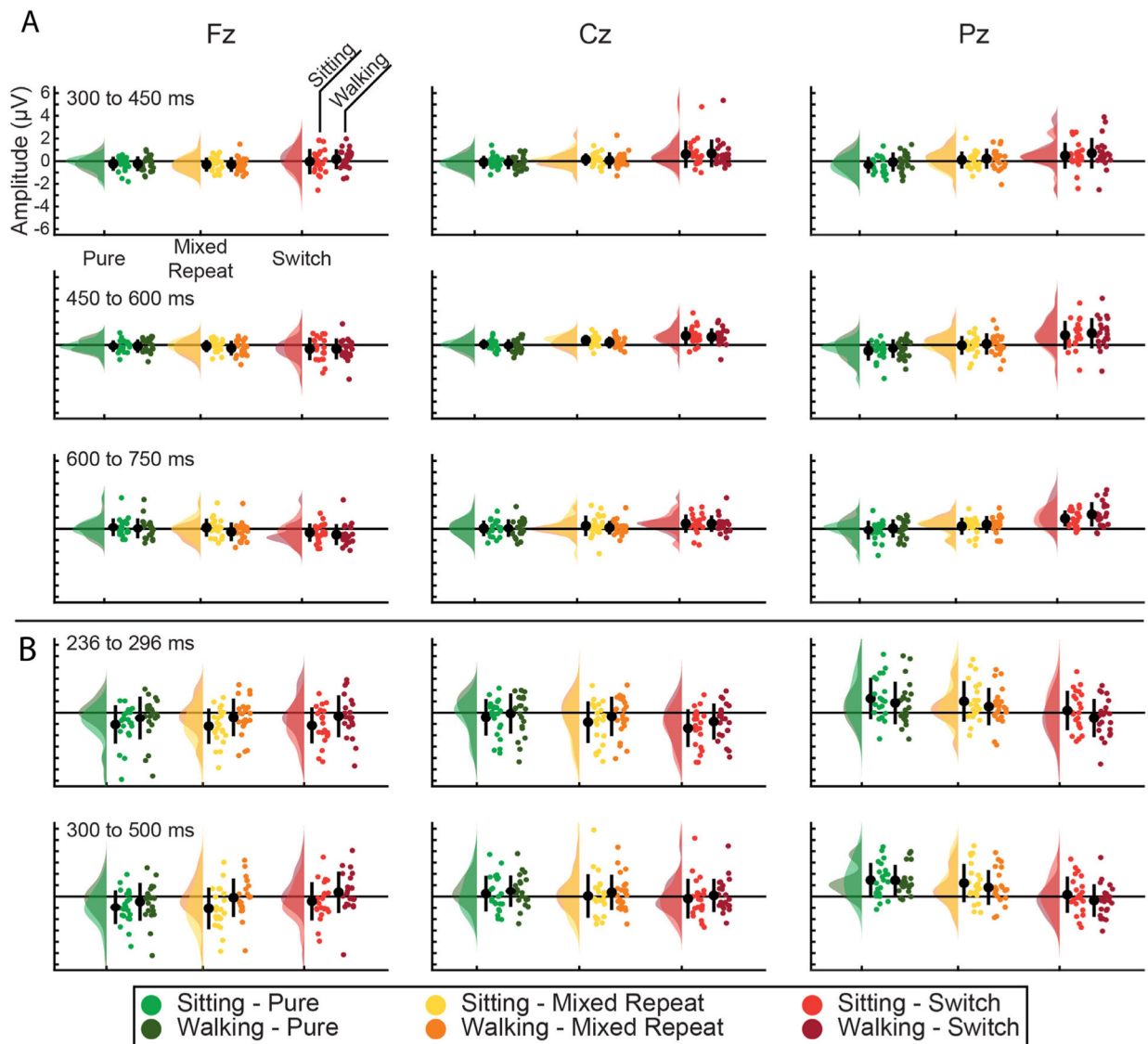
Fig. 5.
Scatter and raincloud plots for CTI (A) and PTI (B) preplanned intervals. Each subplot displays individual participant mean amplitude measurements for each experimental condition at the given time interval (row) and electrode site (column). Group mean +/− 1 SD is indicated by a black dot and whiskers to the left of each data cluster. Cluster pairs are grouped by trial type, juxtaposing measurements collected while sitting (left cluster) against walking (right cluster). Probability density curves ('rainclouds') are displayed to the left of each cluster pair.
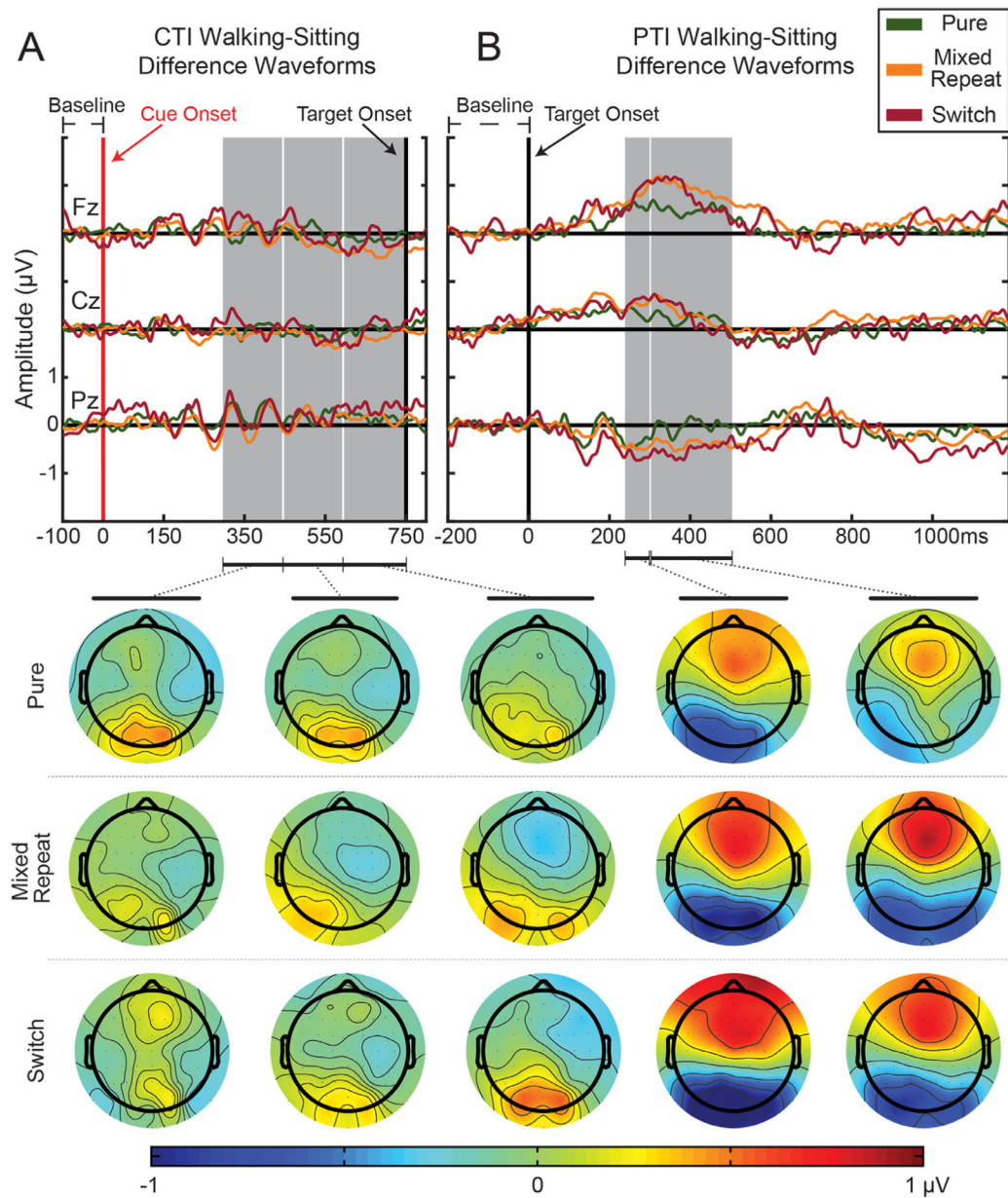
Fig. 6.
Walking-sitting difference waveforms for pure (orange), mixed repeat (maroon), and switch trials (green) in the cue-target interval (A) relative and in the post-target interval (B) are shown. Highlighted regions correspond to the intervals selected for preplanned statistical analysis. Topographical scalp maps displaying mean amplitude at the highlighted CTI and PTI intervals are displayed at bottom of figure.
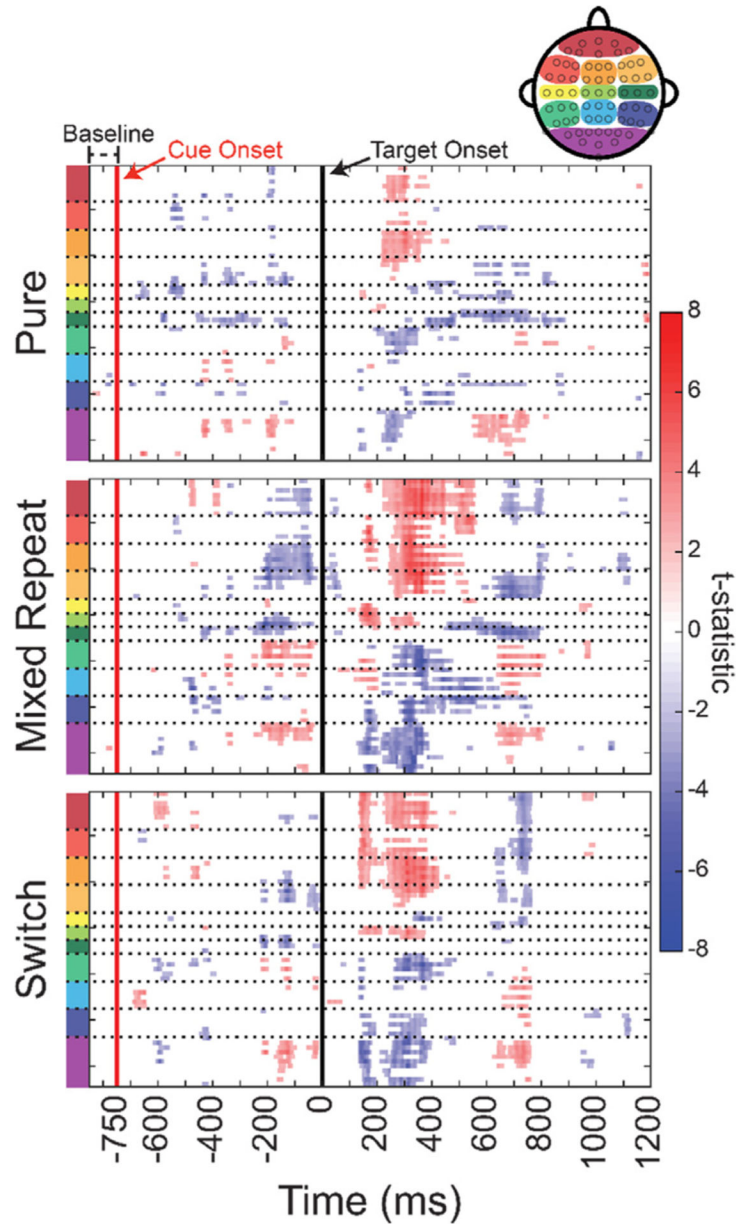
Fig. 7.
Statistical cluster plots displaying CTI and PTI. Data used in analyses are time-locked to target onset with a 100 ms pre-cue baseline. Color values indicate the T-statistic result of pointwise t-tests comparing the walking and sitting conditions for each trial type conducted at each time point (x-axis) and electrode position (y-axis). Spatiotemporal clusters attaining the threshold for statistical significance (11 consecutive tests with $p < 0.05$) illustrate regions and intervals of relative positivity (red) or negativity (blue) in task-evoked potentials recorded during simultaneous walking (with respect to sitting). Plots are organized by cognitive task trial type (from top to bottom): Pure, Mixed repeat, and Switch.

Table 1

Results of repeated measures ANOVAs. All p-values shown are Greenhouse-Geisser corrected for violation of sphericity. Bold text indicates p-value < 0.05. Effect sizes are reported as partial eta squared.

	Time Interval (ms)				
	CTI (100 ms pre-cue baseline)		PTI (200 ms pre-target baseline)		
	−450 to −300	−300 to −150	−150 to 0	236 to 296	300 to 500
Main Effect For Trial Type	$F_{2,42} = 13.43\ p = 0.0005\ \eta_p^2 = 0.390$	$F_{2,42} = 38.89\ p < 0.0001\ \eta_p^2 = 0.649$	$F_{2,42} = 18.41\ p < 0.0001\ \eta_p^2 = 0.467$	$F_{2,42} = 22.46\ p < 0.0001\ \eta_p^2 = 0.517$	$F_{2,42} = 12.88\ p = 0.0004\ \eta_p^2 = 0.380$
Main Effect for Physical condition	$F_{1,21} = 2.46\ p = 0.1319\ \eta_p^2 = 0.105$	$F_{1,21} = 0.02\ p = 0.8955\ \eta_p^2 = 0.001$	$F_{1,21} = 0.11\ p = 0.7464\ \eta_p^2 = 0.005$	$\mathbf{F_{1,21} = 7.99\ p = 0.0101\ \eta_p^2 = 0.276}$	$\mathbf{F_{1,21} = 9.98\ p = 0.0047\ \eta_p^2 = 0.322}$
Main Effect for Electrode	$F_{2,42} = 2.72\ p = 0.1038\ \eta_p^2 = 0.115$	$\mathbf{F_{2,42} = 4.21\ p = 0.0431\ \eta_p^2 = 0.167}$	$\mathbf{F_{2,42} = 4.22\ p = 0.0435\ \eta_p^2 = 0.167}$	$\mathbf{F_{2,42} = 5.10\ p = 0.0280\ \eta_p^2 = 0.195}$	$F_{2,42} = 3.09\ p = 0.0843\ \eta_p^2 = 0.128$
Interaction for Trial Type × Physical condition	$F_{2,42} = 1.22\ p = 0.2971\ \eta_p^2 = 0.055$	$F_{2,42} = 0.78\ p = 0.4467\ \eta_p^2 = 0.036$	$F_{2,42} = 2.67\ p = 0.0850\ \eta_p^2 = 0.113$	$F_{2,42} = 0.30\ p = 0.7272\ \eta_p^2 = 0.014$	$F_{2,42} = 0.56\ p = 0.5652\ \eta_p^2 = 0.026$
Interaction for Trial Type × Electrode	$F_{4,84} = 2.06\ p = 0.1386\ \eta_p^2 = 0.089$	$\mathbf{F_{4,84} = 15.48\ p < 0.0001\ \eta_p^2 = 0.424}$	$\mathbf{F_{4,84} = 18.99\ p < 0.0001\ \eta_p^2 = 0.475}$	$\mathbf{F_{4,84} = 5.91\ p = 0.0082\ \eta_p^2 = 0.220}$	$\mathbf{F_{4,84} = 27.60\ p < 0.0001\ \eta_p^2 = 0.568}$
Interaction for Physical condition × Electrode	$F_{2,42} = 1.10\ p = 0.3232\ \eta_p^2 = 0.050$	$F_{2,42} = 2.37\ p = 0.1276\ \eta_p^2 = 0.102$	$\mathbf{F_{2,42} = 5.87\ p = 0.0167\ \eta_p^2 = 0.218}$	$\mathbf{F_{2,42} = 19.99\ p < 0.0001\ \eta_p^2 = 0.488}$	$\mathbf{F_{2,42} = 16.93\ p < 0.0001\ \eta_p^2 = 0.446}$
Interaction for Physical condition × Trial Type × Electrode	$F_{4,84} = 0.32\ p = 0.7411\ \eta_p^2 = 0.015$	$F_{4,84} = 0.11\ p = 0.8992\ \eta_p^2 = 0.005$	$F_{4,84} = 0.50\ p = 0.6041\ \eta_p^2 = 0.023$	$F_{4,84} = 1.15\ p = 0.3327\ \eta_p^2 = 0.052$	$\mathbf{F_{4,84} = 3.77\ p = 0.0273\ \eta_p^2 = 0.152}$