Asymmetric Interference Between Cognitive Task Components and Concurrent Sensorimotor Coordination

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Abstract

Everyday cognitive tasks are frequently performed under dual-task conditions alongside continuous sensorimotor coordinations (CSC) such as driving, walking, or balancing. Observed interference in these dual-task settings is commonly attributed to demands on executive function or attentional resources, but the time-course and reciprocity of interference are not well understood at the level of information-processing components. Here, we used electrophysiology to study the detailed chronometry of dual-task interference between a visual oddball task and a continuous visuomanual tracking task. The oddball task's electrophysiological components were linked to underlying cognitive processes, and the tracking task served as a proxy for the continuous cycle of state-monitoring and adjustment inherent to CSCs. Dual-tasking interfered with the oddball task's accuracy and attentional processes (attenuated P2 and P3b magnitude, and parietal alpha-band ERD), but errors in tracking due to dual-tasking accrued at a later time-scale, and only in trials in which the target stimulus appeared and its tally had to be incremented. Interference between cognitive tasks and CSCs can be asymmetric in terms of timing as well as affected information-processing components.

Keywords: Dual-tasking, event-related potential, oddball task, tracking, sensorimotor coordination, balancing, walking, gait, driving

New and Noteworthy

Interference between cognitive tasks and continuous sensorimotor coordination (CSC) has been widely reported, but this is the first demonstration that the cognitive operation that is impaired by concurrent CSC may not be the one that impairs the CSC. Also demonstrated is that interference between such tasks can be temporally asymmetrical. The asynchronicity of this interference has significant implications for understanding and mitigating loss of mobility in old age, and for rehabilitation for neurological impairments.

There are many instances in everyday human behavior when a continuous sensorimotor coordination (CSC) occurs concurrently with an intermittent cognitive task. CSC tasks are characterized by sustained, task-constrained patterns of body or limb movements generated by a combination of feedforward and perception-based feedback control processes (Seidler et al. 2004). Performance in CSC tasks, such as driving a motor vehicle, goal-directed walking or even upright standing, must be maintained while carrying out a conversation, a sequence of memory or problem-solving operations, or planning future actions. In the case of driving, such dual-task effects have been of particular research interest with respect to interference from mobile (cellular) telephone conversation (Recarte and Nunes 2003; Strayer and Johnston 2001). Dual-task gait and balance have also been extensively researched as concurrent cognitive load is a recognized risk factor in falling in old age (Amboni, Barone and Hausdorff 2013; Rubinstein 2006), and declining dual-task performance is a salient feature not only of healthy aging (Fraizer and Mitra 2008; Springer et al. 2006), but also the time course of neurological conditions such as Parkinson’s disease (Bloem et al 2001; Yogev-Seligmann et al 2007) and dementia (Ijmker and Lamoth 2012). Recent research has shown that a range of cognitive tasks interfere with everyday CSCs such as driving (Beede and Cass 2006; Nijboer et al 2016; Recarte and Nunes 2003), walking (Al-Yahya et al. 2011; Holtzer et al 2012) and balancing (Fraizer and Mitra 2008), and that the level of interference tends to be greater in old age (Li and Lindenberger 2002). Thus, despite their apparent autonomy in the healthy young and middle-age adults, everyday CSC tasks make demands on higher level cognitive resources.

Suggested neuropsychological mechanisms underlying interference during concurrent cognitive operations include attentional capacity-sharing, whereby performance in multiple attention-demanding tasks deteriorates due to limitations in available processing resources

(Tombu and Jolicoeur 2003), or as a result of information-processing bottlenecks caused by multiple operations requiring access to a common processor or neural network (Ruthruff et al 2001). Multiple resource models (Pashler 1994) have been proposed to explain why interference occurs in certain task combinations (a common resource is accessed) but not in others (the tasks are serviced by separate resources). In the context of CSC-cognitive dual-tasking, the literature on driving (Beede and Kass 2006; Recarte and Nunes 2003; Nijboer et al 2016) and gait (Al-Yahya et al. 2011; Amboni et al 2013) suggests that executive function (EF) operations are the most prone to interference, but research on balancing has been framed in terms of competition for, and allocation of, attentional resources (Redfern et al. 2002; Woollacott and Shumway-Cook 2002). EF broadly refers to higher cognitive processes involved in holding and manipulating task-relevant information in working memory (Baddeley 1996; D’Esposito et al. 1999), and allocating processing resources as required (sometimes termed executive attention) (Baddeley 2007; Norman and Shallice 1986; Royall et al. 2002). In terms of specific information-processing operations, EF includes updating (monitoring and altering WM contents), shifting (switching between task sets) and inhibition of irrelevant information or processes (Miyake et al. 2000; Miyake and Friedman 2012).

Everyday CSC-cognitive dual-task situations present several challenges in terms of precisely identifying the mechanisms underlying behaviorally observed interference. The first challenge, is that it is generally possible to reduce CSC speed (Haigney et al 2000; Al-Yahya et al. 2011) to enable diversion of information-processing cycles or resources to a concurrent cognitive task. When the CSC exhibits slower speed in the presence of a concurrent cognitive task, it can be unclear whether the interference source was at the level of concurrent attentional resource demands or the EF of switching resources between task sets. A CSC task that does not permit such strategic speed variation could help isolate the effects of common information-processing resource demands.

The second challenge is that everyday CSCs have a degree of performance tolerance that can be exploited to fit in the demands of a concurrent cognitive task. For example, highway lane width and walking paths allow a level of trajectory deviation without compromising safety or overall task goals (Nijboer et al. 2016; Springer et al. 2006). It is usually possible to strategically allow a level of error to accumulate in order to fit in the demands of a secondary task. A CSC task that isolates the use of perceptual information to continuously stabilize the coordination (i.e., exposes all deviations as error) could help locate the precise loci of interference between processes of CSC maintenance and the operations of a concurrent cognitive task.

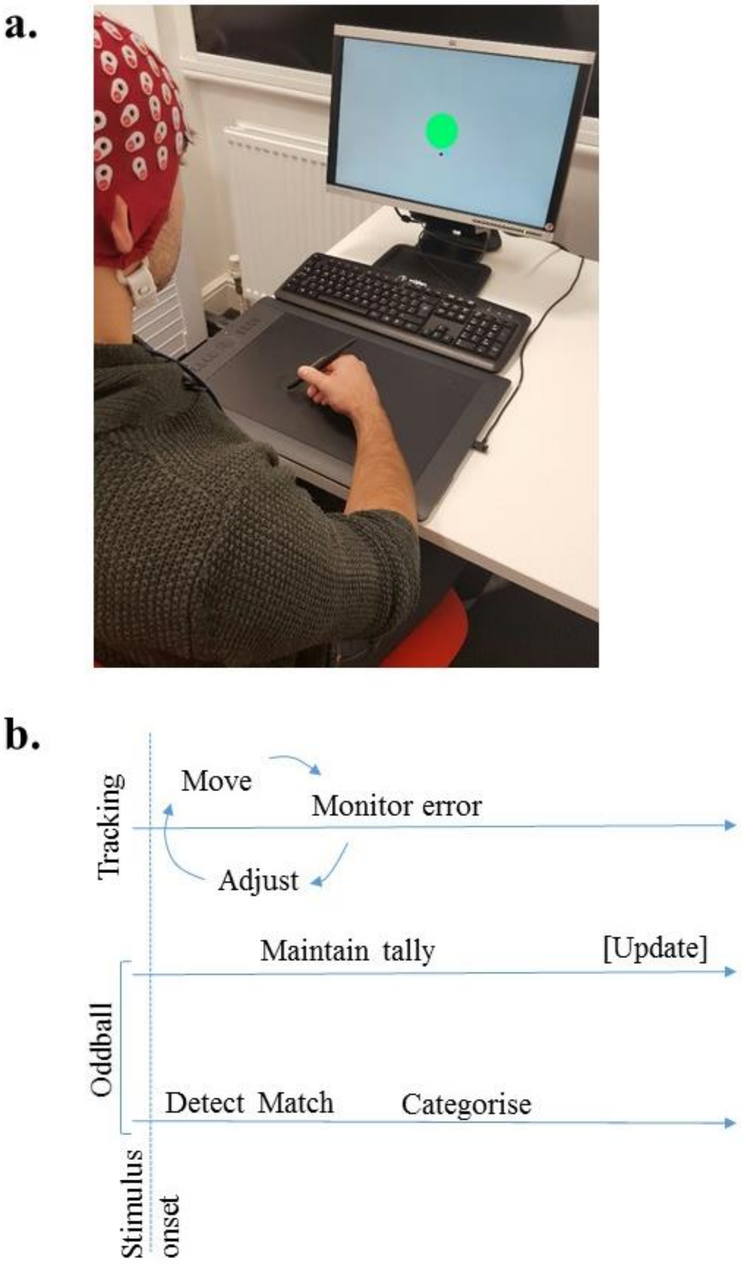
The third challenge in understanding CSC-cognitive dual-task interference is that most everyday cognitive tasks involve perceptual, attentional and executive function sub-processes. Interference between such tasks and CSCs may affect one or more of these sub-processes, and the effects may or may not be symmetrical. Behavioral measures such as accuracy or response time in cognitive tasks, and the variability of lane deviation, stride length or body sway, cannot by themselves resolve the chronometric details of these interactions as they reflect the cumulative effects of the tasks’ central and response-related information-processing components. If the sequence of neurophysiological events associated with the sub-processes of a cognitive task are known and observable, investigating these events’ interactions with a CSC stabilization task could provide a more detailed understanding of the structure and timing of CSC-cognitive interference.

Here, we addressed these challenges by asking participants to perform a visuomanual pursuit-tracking task (Chernikoff et al. 1955), and used electrophysiological techniques to investigate the chronometric details of this CSC's interactions with the extensively studied cortical dynamics of the visual oddball task (Fig. 1). The key interest in this task combination was that the timing and reciprocity of influence from either task to the other could be studied at the level of component processes. It is seldom clarified whether, for example, the attentional component of a cognitive task that is disrupted by a concurrent CSC is also the cognitive task component that disrupts CSC performance. Addressing the outlined challenges and utilizing the high temporal resolution of electrophysiological events enables the present study to detect possible asymmetries in interference at the level of task components.

Pursuit-tracking has a long history of use in studies of dual-task interference (e.g., Brown 1998; Gazes et al. 2010; Isreal et al 1980; Kramer et al 1983;), including as a simulated driving task (e.g., Strayer and Johnston, 2001), and as a secondary task during postural perturbations (e.g., McIlroy et al. 1999; Norrie et al. 2002). In the laboratory, pursuit-tracking involves continuously minimizing the positional error between a manually controlled cursor and an independently moving, computer-controlled visual target on a screen (Brown 1998; Gazes et al. 2010). Our use of pursuit-tracking addressed the first two challenges identified above by enforcing the maintenance of CSC speed, and allowing no strategic trajectory deviation or variability without accumulating detectable horizontal and vertical positional errors.

To address the issue of sub-processes, we incorporated a visual oddball task as the concurrent cognitive task. The oddball task required an action only when the less frequent of two possible stimuli was detected (Hillyard et al. 1973). The template for the target stimulus had to be maintained in WM and matched to the current perceptual stimulus. This involved top-down facilitation of matching features and inhibition of non-matching ones (D’Esposito and Postle 2015). As a physical response (such as clicking a button or pressing a foot pedal) could introduce an additional motor interference, the participants instead produced a cognitive response–mentally tallying the number of targets detected over the current block of trials. This covert-response variant of the oddball task has an electrophysiological signature analogous to that of the overt, motor-response version in the stimulus processing phase (Potts 2004; Salisbury et al. 2001; Verleger et al. 2016), but it also involves an additional WM component of maintaining the current target count, and an executive function of updating (Garavan et al. 2000) the tally every time a target is identified (Fig. 1).

FIGURE 1



The oddball task is well suited to studying dual-task interference at the level of information-processing components because extensive research has linked its electrophysiological correlates to the time course of its underlying cortical processes (Polich 2007). We consider event-related potentials (ERP) first, followed by spectral characteristics of EEG data. Three event-related potential (ERP) components express the key features of information processing in this task. P1 occurs around 100 ms post-stimulus-onset over occipital sites, and is sensitive to bottom-up stimulus characteristics such as brightness or contrast (Johannes et al. 1995). P2 occurs anteriorly about 200 ms post-stimulus-onset, and is thought to represent top-down mechanisms by which the current stimulus is compared to representations of previous ones (e.g., known templates for standard and target stimuli) (Kim et al. 2008; Luck 2005). The P3b occurs 300-400 ms post-stimulus-onset and is thought to correspond to stimulus categorization (that it is a target), and acknowledgement of task relevance (that the tally requires updating) (Polich 2007; Luck 2014). Previous research suggests that, if concurrently performing the tracking task impedes only the top-down aspects of oddball task performance, only P2 and P3b, but not P1, will be attenuated (Allison and Polich 2008; Isreal et al. 1980; Kida et al. 2004; Matthews et al. 2006). In this study, we used target stimuli (shaded circles) with greater contrast than the standard stimuli (unshaded circles), such that a bottom-up stimulus effect might be expected for P1 (Johannes et al. 1995), but not a dual-task effect, unless the tracking task also degraded the bottom-up perceptual processing of the oddball stimulus.

The oscillatory characteristics of cortical networks underpinning oddball task performance can be examined through event-related spectral perturbations of EEG recorded from parietal and frontal sites (Makeig et al. 2004). At parietal sites, an event-related desynchronization (ERD) in the alpha band (8-13 Hz) occurs approximately 400-600 ms post-stimulus-onset when a change in processing is required, such as when the rarer target as opposed to the standard stimulus appears (Sutoh et al. 2000). If the detection of this change is impaired by dual-tasking, parietal ERD ought to be attenuated. Also, a larger alpha-band response to a target as opposed to a standard stimulus is known to occur at anterior locations at these latencies (Yordanova and Kolev 1998; Başar and Güntekin 2012). Alpha power at fronto-central sites in tasks involving WM processes is thought to reflect inhibition of task-irrelevant information (Klimesch et al. 1998). However, recent work using post-cuing paradigms, that allow systematic manipulation of relevant and irrelevant WM load (Manza et al. 2014), suggest that fronto-central alpha power reflects maintenance of task-relevant WM load, and is related to task accuracy. Either way, if dual-tasking added to WM load, then an increase in frontal alpha power (alongside lowered accuracy) would be expected.

Coordination in the fronto-parietal network (Corbetta and Shulman 2002) underpinning attention and WM tasks (such as oddball detection) is electrophysiologically reflected in alpha-band coherence between frontal and parietal sites (Sauseng et al. 2006; Güntekin and Başar 2010; Sadaghiani et al. 2012; van Schouwenburg et al. 2017). Güntekin et al (2008) have shown, for example, that impaired cortical connectivity in Alzheimer's reduces fronto-parietal alpha-band coherence in a visual oddball task. If concurrently performing visuomanual tracking reduces the effectiveness of the fronto-parietal network, a lower level of alpha coherence would be expected.

Turning to the effects of the oddball task on pursuit-tracking, if the oddball task reduces motor programming resources for pursuit-tracking, we might observe differences in spectral power over contralateral motor cortex relative to the tracking-only condition. Manual task execution is accompanied by an event-related desynchronization (ERD) over contralateral primary motor cortex characterized by reduced power in the alpha (7-13 Hz) and beta (13-30 Hz) bands (Pfurtscheller and Lopes da Silva 1999). If concurrent performance of the oddball task reduces resourcing of the tracking task, we would expect reduced ERD (i.e., higher spectral power) over contralateral motor cortex during dual-tasking relative to performing tracking by itself.

In terms of tracking performance, any disruption resulting from the concurrent oddball task would be detectable as vertical and horizontal positional deviations from the set trajectory. More importantly, the timing of such deviations would be highly informative in time-locked juxtaposition with the electrophysiological indicators of the oddball task's cortical processes (see Fig. 1). Positional error accruing in the P2 timescale would be indicative of a top-down attentional process in a concurrent cognitive task that disrupts tracking. Deviation in the P3b timescale would implicate the processes of task-relevance judgement. If error build-up occurs later still, then the executive function of updating (incrementing the target count) would be the most likely interference source.

In summary, we hypothesized that performing the tracking task concurrently with the oddball task would not affect the oddball task at the P1 timescale, but would attenuate P2 and P3 amplitudes, indicating reduced attentional resourcing of oddball task performance. We also expected that dual-tasking would attenuate parietal alpha-band ERD, indicating impaired target detection in the oddball task. Further, we expected an increase in frontal alpha power (and lower accuracy) in the dual-task target condition, confirming an overall increase in WM load in that condition. Also, we expected to see reduced fronto-parietal alpha-band coherence in the dual-task condition as an indication of degraded resourcing in the dual-task condition.

The above hypotheses were derived from the expectation that the concurrent tracking task would impede resourcing of the oddball task. In the reverse direction, if the cognitive task load interfered with tracking, we expected to see positional errors develop at the time periods of this interference. Also, if the concurrent oddball task negatively impacted resourcing of the tracking task, we expected to observe weaker ERD over contralateral motor cortex in the dual-task condition.

The key interest in this work lies in the symmetry and synchrony of the expected interference. If the component of the oddball task that had a negative impact on tracking was also the task component that was impaired by tracking, we would have expected these reciprocal effects to be synchronous. On the other hand, if, say, tracking affected the attentional components of the oddball task, but it was the later executive function component of the oddball task that impaired tracking, then we would have expected to see temporally separated directional effects on electrophysiological components and task performance.

Materials and Methods

Participants

The participants were 24 self-reportedly right-handed adults (13 females; mean age = 25.6 years, SD=6.13, range 19-42), with normal or corrected to normal vision, no current prescribed medication, and no history of sensorimotor or cognitive deficits. They were recruited through a research participation scheme for students, and given research credits in return for their participation. The participants gave informed consent before the session, and were fully debriefed at the end. Ethical approval for the research reported in this paper was granted by the Nottingham Trent University College of Business, Law and Social Sciences Research Ethics Committee.

Apparatus and Experimental Procedure

The participants sat in a comfortable and stable chair with their eyes positioned approximately 60 cm from the center of a 19” (48.26 cm) diagonal color LCD screen displaying 1600 x 900 pixels at 60 Hz (Fig. 1a). After explaining the required tasks and the structure of the session, the experimenter obtained written informed consent, and then administered a motor configuration task to establish the participants' comfortable visuomanual tracking speed. The participant was then prepared for EEG data recording using a 128-channel ActiveTwo Biosemi system (Amsterdam, The Netherlands). Electrodes were placed in the Biosemi ABC configuration using an elastic cap fitted to the participant's head. The participant then performed the visuomanual tracking, visual oddball and dual-task sessions. To prevent practice and fatigue factors from affecting differences between these three task conditions, the order of these sessions was counterbalanced across participants. Participants were instructed to fixate at the center of the display (fixation cross) at all times for each of the task conditions and to avoid looking at the moving dot and curser.

Motor task configuration

With eyes fixated at the center of the screen, the participants used a Wacom Intuos Pro digitizing tablet and stylus (Saitama, Japan) to pursue a small cyan-colored leading dot (r = 25 pixels) rotating clockwise in a circle (r = 130 pixels; 36 mm) around a fixation cross (see Figure 1a). Participants were positioned so that their eyes were approximately 800-850 mm from the fixation cross on the screen, so the leading dot's track subtended a visual angle of 2.42°-2.57° with eyes at fixation. Note that the ability to split covert attention between spatial locations has been tested at up to 3.5° of eccentricity from fixation (e.g., McMains and Somers 2004). The stylus' position was represented on screen as a black dot (r = 20 pixels), and the participant's task was to move the stylus over the tablet so as to keep the black, controlled dot overlaid on the leading cyan dot throughout the trial duration (10 s). Seven trials were presented sequentially in which the angular velocity of the leading dot increased from 84 degrees per second (dps) in the first trial to 168 dps in the seventh trial (in 12 dps increments). The same seven trials were then presented in reverse order. For each trial, the proportion of the final 7 seconds of trial time during which the two dots overlapped in horizontal (x) and vertical (y) coordinates was calculated. The angular velocity at which a participant produced their third best tracking performance was taken as that participant's comfortable visuomanual tracking speed. The participants' chosen velocities ranged from 96 dps to 144 dps. The most common comfortable speed was 120 dps.

Visuomanual tracking task

The participants performed the visuomanual tracking task at their comfortable speed (as determined earlier by the configuration task). This part of the session consisted of 8 blocks, each lasting 120 s. The screen coordinates of the leading and controlled dots, and the participants' EEG data were recorded.

Visual oddball task

The participants fixated at the center of the screen while a sequence of shaded (target) or non-shaded (standard) circles (r = 100 pixels) were presented, centered on the fixation cross (Fig. 1a). These stimuli were presented for 200 ms, with an ISI of 2500 ms (Fig. 1b). The ratio of target to standard stimuli was 1:4, and there were at most 12 targets presented in each block (the number of trials per block varied between 40 and 60). The participants' task was to silently count up the number of targets presented in a block, and report it via the keyboard once the block had finished. There were 8 blocks of trials in total and the number of blocks in which the number of targets were counted correctly was recorded, as were the participants' EEG data. Accordingly, accuracy on the oddball task was recorded as either a 1 (accurately reported the number of targets in the block), or 0 (did not report the correct number of targets in the block), for each of the 8 blocks.

Dual-tasking

The participants performed the visual oddball task whilst also performing the visuomanual tracking task. Each block of trials started with the leading and controlled dots in an overlapping position. As the leading dot started moving, and the oddball task got under way, the participants' task was to maintain the positional overlap between the dots while performing the oddball task. The coordinates of the controlled and leading dots, the target count and the EEG data were recorded. As in the single-task conditions, the instruction throughout was to maintain eye fixation on the cross at the center of the screen.

Experimental Measures and Analyses

Oddball detection performance

Performance on the oddball task was taken as the proportion of blocks in which participants correctly counted all of the target stimuli presented. Accuracy on a given block was reported as either a 1 (correctly reported the number of targets presented), or a 0 (incorrectly reported the number of targets). Overall oddball task performance for each participant for each condition (single and dual task) was calculated as a percentage of correct blocks out of all of the possible 8 blocks.

Visuomanual tracking deviation analysis

The instantaneous positional discrepancy (in pixels) between the leading and controlled dots in the visuomanual tracking task was calculated as horizontal (X) and vertical (Y) deviation. For each frame, the quadrant in which the lead dot was located was used to calculate the sign of the deviation such that it would always have a negative value when the controlled dot trailed the lead dot, and vice versa (e.g., deviation(X) = controlled(X) – lead(X) in quadrants

I and IV, but deviation(X) = lead(X) – controlled(X) in quadrants II and III). Deviation in the vertical axis was also calculated using analogous arithmetic. Deviation samples were epoched around the oddball stimulus onset (-150 to 1500 ms). In the condition with only the visuomanual tracking task, deviation samples were epoched using the visual oddball task's timeline just as in the case of the dual-task condition, except that the oddball task stimuli were not displayed.

EEG data acquisition

EEG data were acquired using 128 Ag/AgCl active pin electrodes at 2048 Hz and digitised with 24-bit resolution. Data were referenced online using a CMS/DRL feedback loop with online low pass filtering performed in the Analogue-Digital-Converter (5th order sinc response with a -3 dB point at 1/5th of the sampling rate). Electrode offsets (difference in µv of each channel from CMS electrode) were examined after electrode application and addressed if the absolute value was >20µV. Digital markers (event codes) were inserted into the continuous EEG via a DB25 cable through a USB-Parallel port interface (Neurospec AG, Switzerland).

EEG data pre-processing and epoching

Continuous EEG data were imported and processed in bespoke scripts using functions from EEGLAB (Delorme and Makeig 2004). Data were down sampled to 256Hz, high-pass filtered at 1 Hz and low-pass filtered at 50Hz using a linear finite impulse response filter. Line noise (50Hz and 100Hz harmonic) was estimated and removed from each channel using CleanLine (Mullen 2012). Linear trends were removed from the data by removing the mean of each channel. Noisy channels were identified from datasets by visual inspection for residual high frequencies and extreme values and then eliminated. Channels with kurtosis over 5 SD from the mean kurtosis of all channels were also removed. EEG epochs were generated by extracting data for -150 to 1500 ms around each event (oddball stimulus onset). EEG epochs were manually searched for artefacts and were removed if they were considered to contain low frequency drifts and/or high frequency activity considered to be biomechanical. EEG was finally re-referenced to an average of all channels followed by the removal of one channel (D32) from each dataset. Re-referencing to an average of all channels reduces the data rank to n-1 and can produce artefactual/duplicate independent components. Removing one (D32) channel corrected for this.

Independent components analyses for artefact rejection

Independent Components Analysis (Infomax ICA;(Bell and Sejnowski 1995)) was applied to EEG epochs to identify neural components contributing to the observed scalp data. ICA involves the linear de-mixing of signals measured across the scalp and is able to separate out and identify electrical sources that are maximally temporally independent, thus allowing the analyses of neural functions in source space (as opposed to sensor space). Component properties (time-series, spectra, topography) were explored in order to identify ocular and muscle components. Ocular components such as blinks and lateral eye movements were identified by low-frequency, non-time-locked fluctuations in the EEG epochs with strong power toward the front of the scalp. Muscle components were identified by high frequency activity in the EEG epochs with concentrated activity close to the jaw. Any suspect ocular and muscular components identified as artefactual during this process were removed from the EEG data structure, thus removing their contributions to the observed EEG.

Event-related potential (ERP) analyses

The EEG epochs were baseline-corrected by removing the mean of a baseline period (-150 ms to stimulus onset) from the entire epoch. A series of frames displaying grand average voltage distribution over the scalp was produced from 0 to 1000 ms post stimulus-onset in 5 ms intervals for each condition. These frames were stitched together to produce an animation of scalp topography. The locations of maximum voltage in the time-range 80-120 ms, 180-220 ms, and 380-420 ms were used to determine electrode clusters for the extraction of component measurements. A virtual electrode approach (Foxe and Simpson 2002; Rousselet et al. 2010) was used to generate ERPs consisting of the maximum value over a cluster of electrodes at each time point throughout the epoch. This approach accounts for individual differences in which electrodes respond maximally to task stimuli (Rousselet et al., 2010).

Difference wave ERPs for each participant were generated by subtracting the standard stimulus response from the target stimulus response for both single and dual task conditions. This resulted in waveforms representing the difference in target and standard stimulus processing. P1 amplitude was quantified as the maximum difference (µv) within the 80-120 ms post stimulus period across a right occipital electrode cluster containing B7, B8, B9, A26, A27 and A28 electrodes. P2 amplitude was quantified as the maximum difference (µv) within the 180-220 ms post stimulus period across a midline fronto-central electrode cluster containing C26, C20, C13, C25, C21 and C12 electrodes. P3b amplitude was quantified as the maximum difference (µv) within the 300-500 ms post stimulus period across a midline parietal cluster containing A5, A19, A32, A18, A20 and A31 electrodes. P1, P2, and P3b latency were taken as the times (ms) of the respective maximum differences.

Time-frequency representation and cross-channel coherence of EEG waveforms

The newtimef function in EEGLAB (Delorme and Makeig 2004) was used to carry out zero-padded FFTs with hanning window tapering to estimate the spectral composition of the EEG signal. For each participant, a time-frequency matrix was produced containing log power (dB) values of 100 frequencies in the 3-45 Hz range over the -150-1500 ms period of each epoch. Average log power values in the 7-13 Hz were taken as alpha-band power. Cross-channel coherence was used to quantify the instantaneous coupling of the amplitude and phase of alpha oscillations between frontal (C21) and parietal (A19) sites. Coherence matrices for both amplitude and phase were generated for each participant, giving a coherence coefficient for each frequency at each time point.

Spectral power over motor cortex

The spectopo function in EEGLAB was used to derive alpha and beta power spectral density at left hemisphere (D19) and right hemisphere (B22) sites (corresponding to C3 and C4, respectively, in the International 10-20 system) during single-task and dual-task standard and target (oddball task) trial periods, and during the single-task motor-only trial periods. Also, alpha and beta power in the dual-task standard and target, and single-task motor task conditions was calculated for six time bins (0-200, 200-400, 400-600, 600-800, 800-1000, and 1000-200 ms) to test for any power differences that may have occurred over shorter durations and therefore could not be detected across whole trial periods.

Results

Oddball target detection accuracy

A paired-samples t-test using an empirical logistic transformation (c=0.001) was conducted to compare target detection accuracy (%) in both single and dual-task conditions. Accuracy was greater in the single (*M*=72.17, *SD*=16.65) than dual-task condition (*M*=48.21, *SD*=20.39); *t*(23)= 2.81, *p*<.001. M1-M2 (back-transformed) = 0.78, *CI* [0.58 0.91].

ERP components

The effects of dual-tasking on the amplitude and latency of P1, P2 and P3b difference waves were analysed using paired sample t-tests (Figs. 2, 3). The P1 difference wave's amplitude did not differ between single and dual task conditions (*t*(23) = 1.36, *p*=.19), but P2 (*t*(23) = 4.02, *p*<.001) and P3 (*t*(23) = 4.03, *p*<.001) difference waves' amplitudes were smaller during dual tasking. As standard and target stimuli (unfilled and filled circles, respectively) differed in bottom-up stimulus characteristics such as brightness and contrast, a stimulus effect on P1 was expected regardless of task conditions. P1 amplitude was indeed greater for target than standard stimuli under both single-task (t(23) = 7.58, p<.001) and dual-task (t(23) = 4.43, p<.001) conditions.

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469 **FIGURE 2**

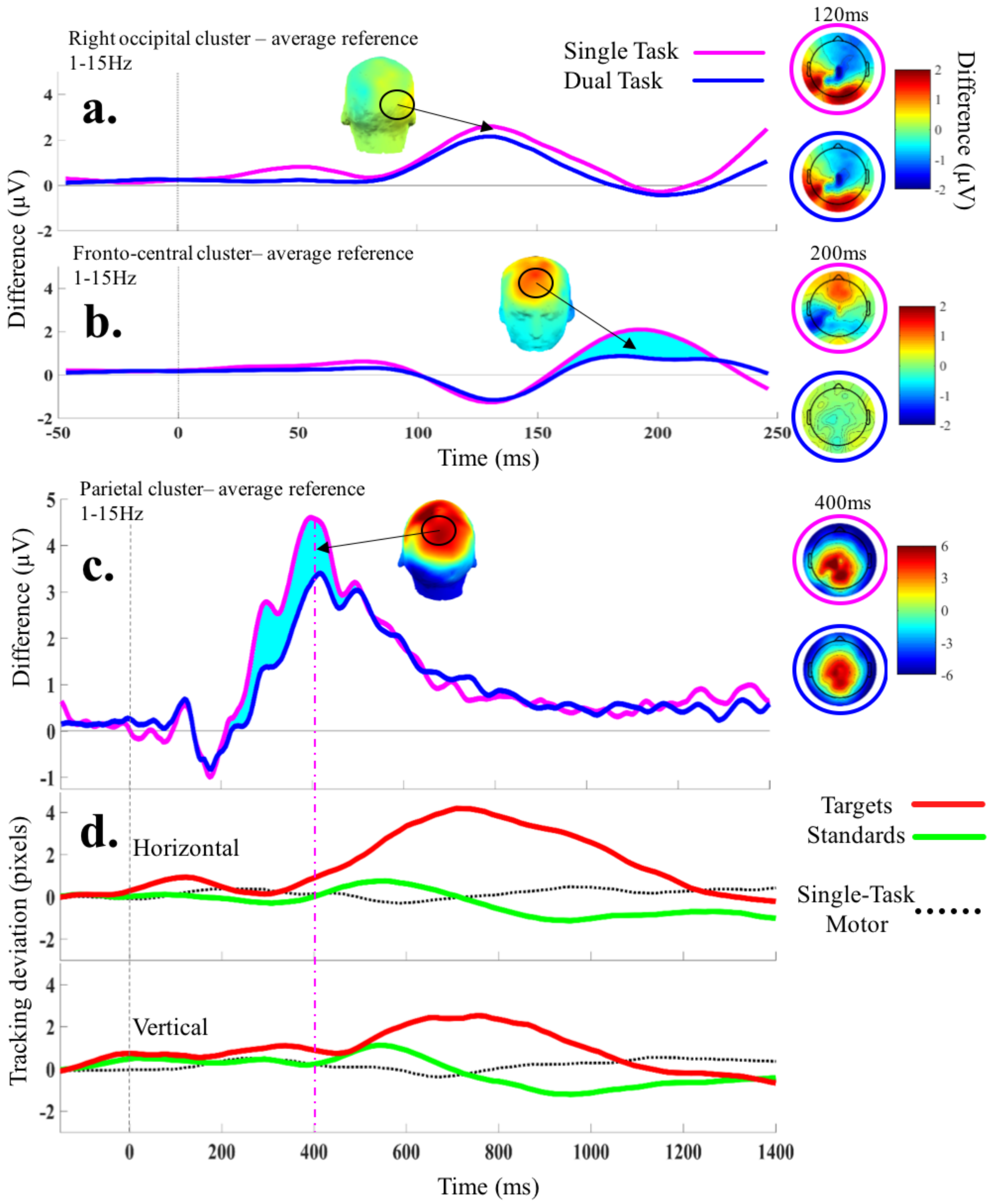

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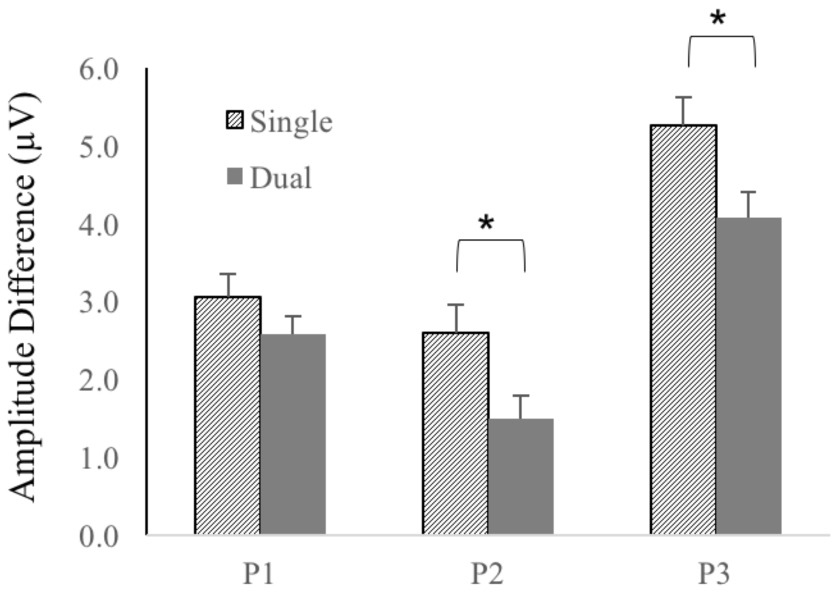
FIGURE 3



Relationship between P2 and P3b amplitude and tracking speed

As participants differed in their preferred tracking speed (speed ranged from 96 to 144 dps), we tested whether participants' P2 and P3b components have been affected by the value of tracking speed. Neither P2 (r=.06, *p*=.77) nor P3b amplitude (r=-.07, *p*=.77) was significantly correlated with tracking speed.

Spectral characteristics of EEG and visuomanual tracking deviation data were analyzed using repeated measures ANOVA with the significance level for omnibus effects set to $p<.05$. A Bonferroni correction was applied (.05/n; n = number of mean comparisons) to post hoc tests using Fisher's LSD. Generalized eta square (η_G^2) (Olejnik and Algina 2003) was used as the effect size statistic.

Parietal and frontal alpha-band power and fronto-parietal alpha-band coherence. Experimental effects on parietal and frontal alpha-band power, and fronto-parietal alpha-band amplitude and phase coherence were analysed using a 2 (Task: single, dual) x 2 (Stimulus: standard, target) x 20 (time) repeated measures ANOVA. Time bins were of 50 ms duration and spanned 0-1000 ms post stimulus onset. Frontal alpha-band power was analysed over the 550-1000 ms time period (as previously discussed).

Parietal alpha-band power

On parietal alpha-band power, there were significant main effects of task (F(1, 23) = 4.75, $p<.05$, $\eta_G^2 = .031$), stimulus (F(1, 23) = 70.13, $p<.01$, $\eta_G^2 = .021$), and time (F(19, 437) = 20.62, $p<.001$, $\eta_G^2 = .132$), and significant task x stimulus (F(1, 23) = 6.04, $p<.05$, $\eta_G^2 = .010$), task x time (F(19, 437) = 3.48, $p<.001$, $\eta_G^2 = .013$), stimulus x time (F(19, 437) = 12.51, $p<.001$, $\eta_G^2 = .038$), and task x stimulus x time (F(19, 437) = 5.97, $p<.001$, $\eta_G^2 = .011$) interactions. As shown in Figs. 4 and 5, the desynchronization in the 450-650 ms period that was observed for target stimuli in the single task was attenuated in the dual task. There was no corresponding pattern in the case of standard stimuli.

FIGURE 4

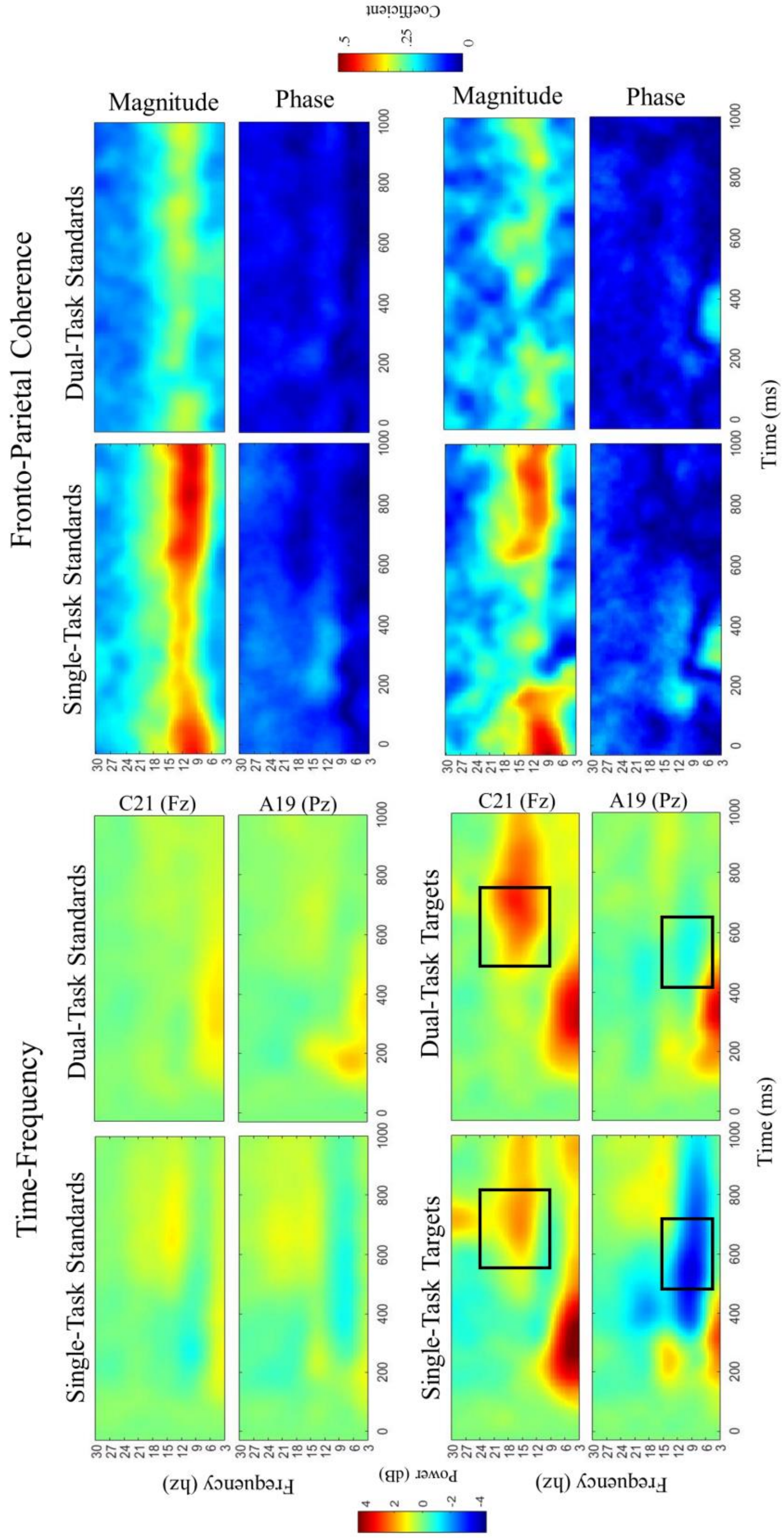
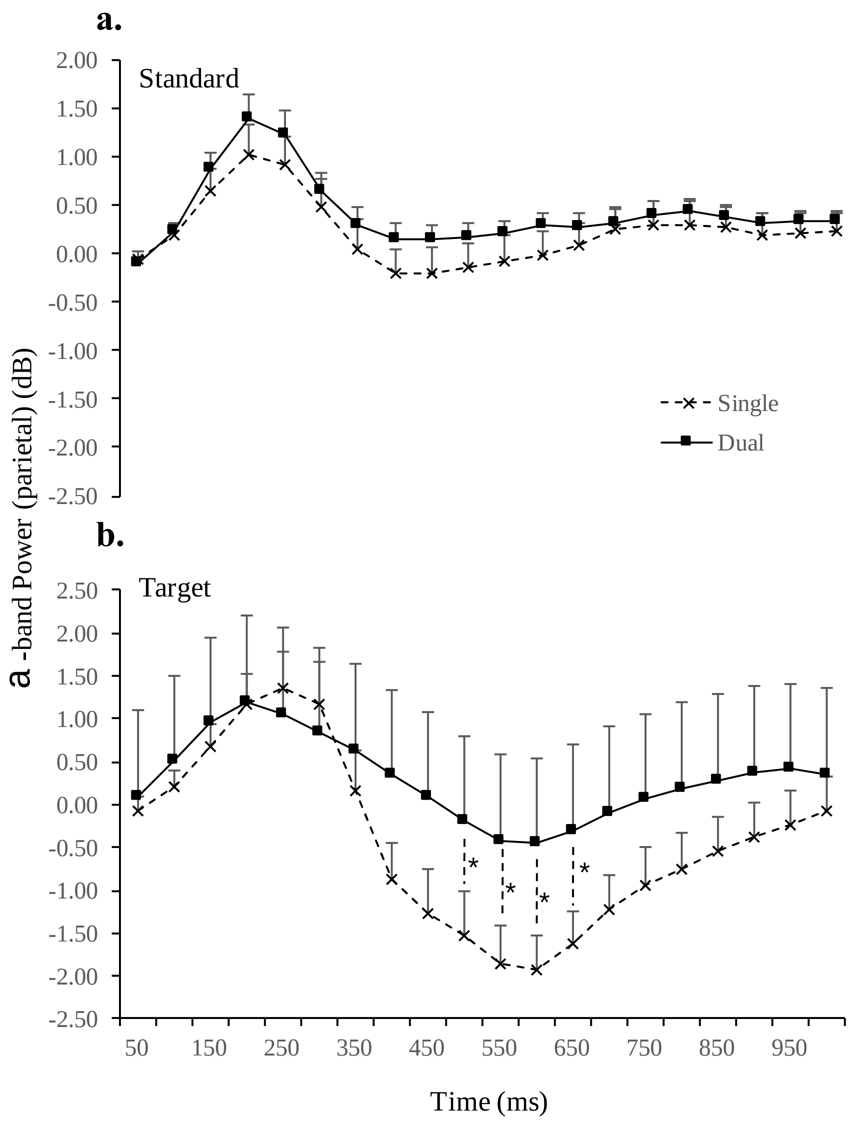

Time-Frequency
Single-Task Standards
Dual-Task Standards
Single-Task Targets
Dual-Task Targets
C21 (Fz)
A19 (Pz)
Frequency (hz)
30 27 24 21 18 15 12 9 6 3
Time (ms)
0 200 400 600 800 1000
Power (dB)
4 2 0 -2 -4
Fronto-Parietal Coherence
Magnitude
Phase
Coefficient
.5 .25 0

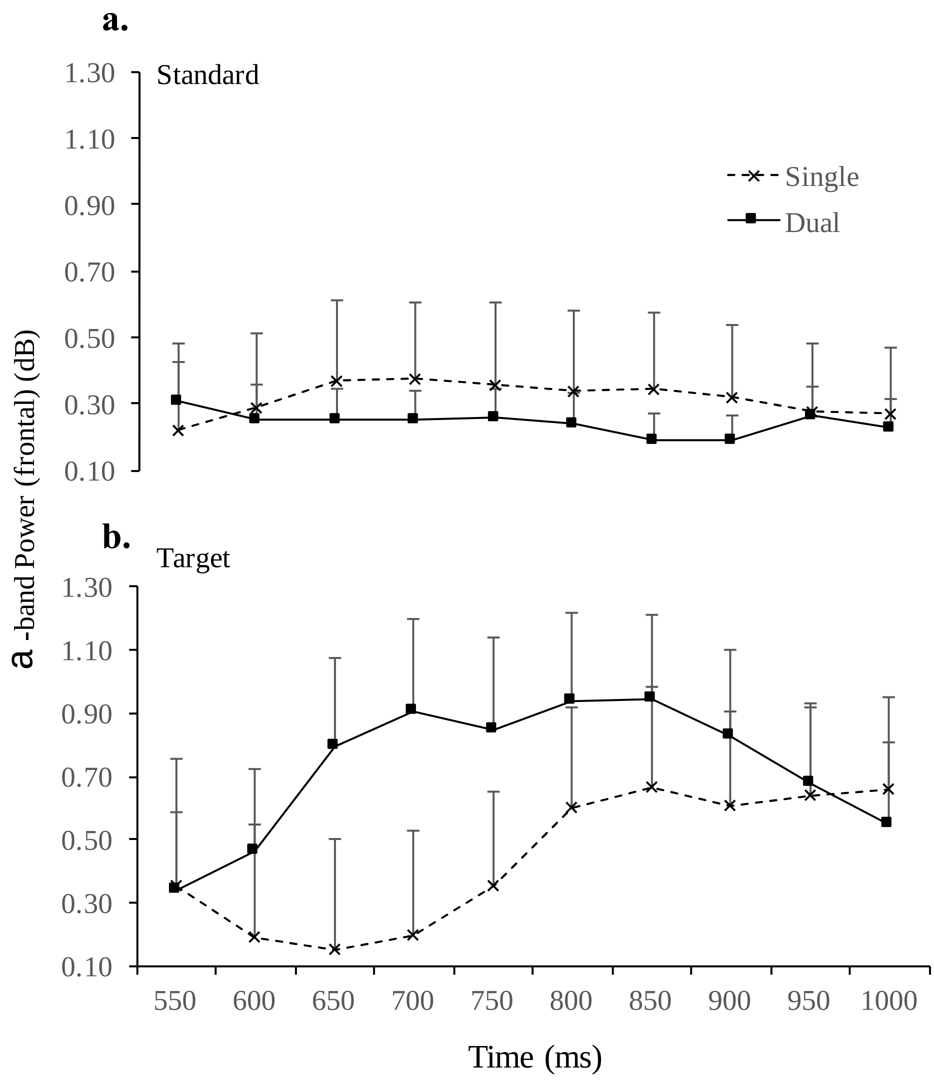
FIGURE 5



Frontal alpha-band power

On frontal alpha-band power, there were significant stimulus x time (F(9, 207) = 2.28, p<.05, η_G^2= .006), and task x stimulus x time (F(9, 207) = 3.17, p<.001, η_G^2= .005) interactions. Frontal alpha-band power was greater in the dual than single task for target stimuli, particularly in the 650-750 ms period (Figs. 4, 6). There was no corresponding difference for the standard stimuli.

FIGURE 6

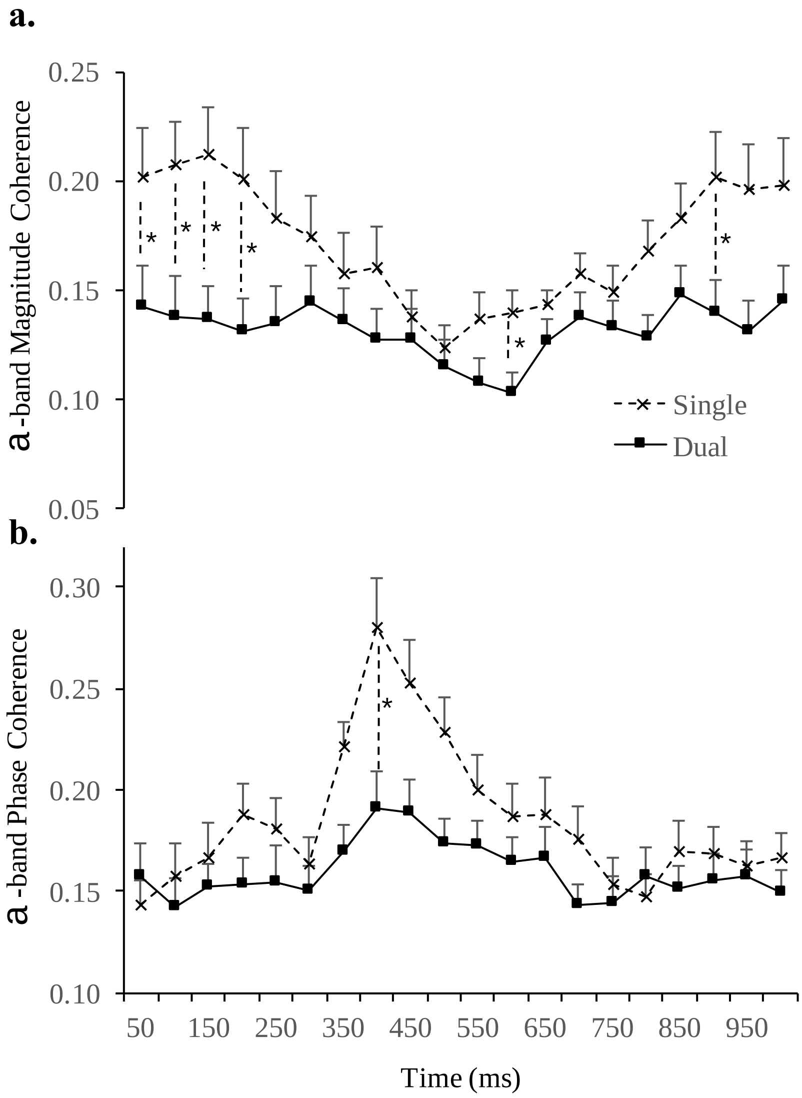


Fronto-parietal alpha-band coherence

On amplitude coherence, there were significant main effects of task (F(1, 23) = 31.99, p<.001, η_G^2= .014) and time (F(19, 437) = 6.25, p<.001, η_G^2= .011), and significant interactions between task and time (F(19, 437) = 2.72, p<.001, η_G^2= .037) and stimulus type and time (F(19, 437) = 2.17, p<.001, η_G^2= .003). The time profile of amplitude coherence was similar in single and dual task, with a period of attenuation centered around 500 ms post stimulus-onset, but overall, coherence amplitude was lower during dual tasking (Figs. 4, 7a). In the case of phase coherence, there were main effects of task (F(1, 23) = 13.29, p<.001,

η_G^2 = .004), stimulus (F(1, 23) = 59.11, p<.001, η_G^2 = .016) and time (F(19, 437) = 10.01, p<.001, η_G^2 = .017), and significant task x time (F(19, 437) = 1.79, p<.001, η_G^2 = .015) and task x stimulus x time (F(19, 437) = 2.5, p<.001, η_G^2 = .001) interactions. The three-way interaction was due to the spike in phase coherence that occurred for target stimuli in the single task, but was not matched during dual-tasking (Figs. 4, 7b).

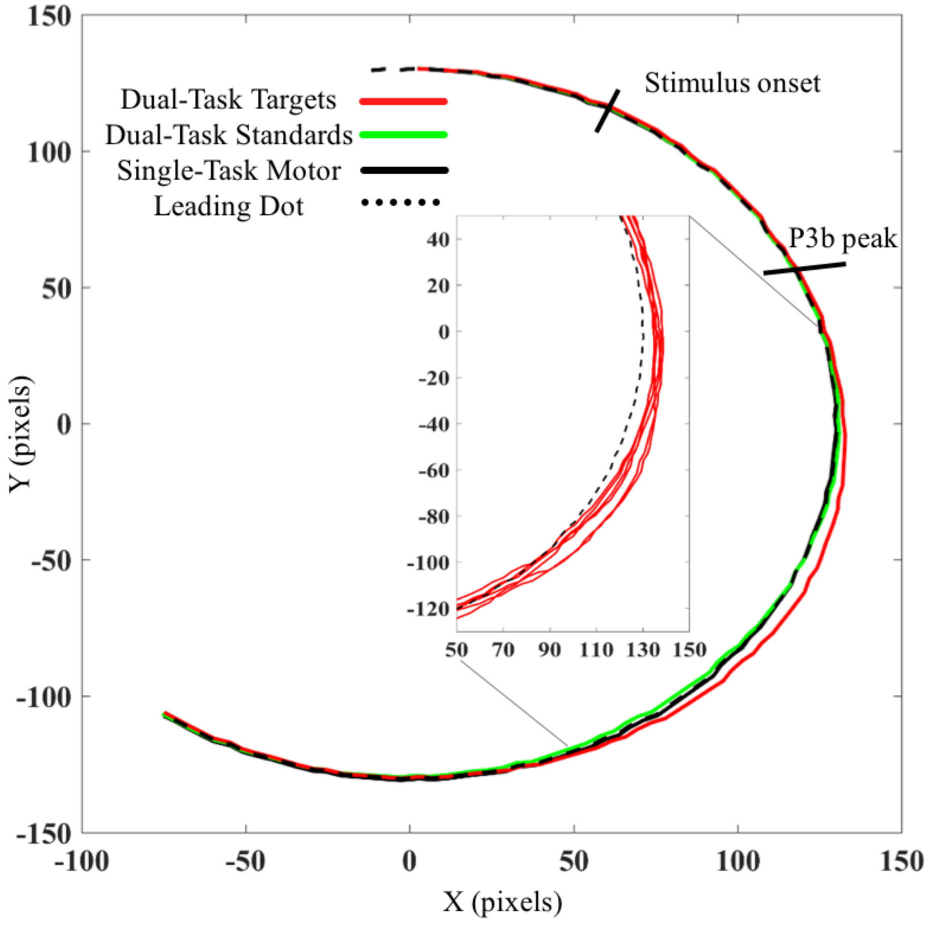
FIGURE 7



Visuomanual Tracking Deviation

Tracking performance during the single and dual task conditions is shown on the timeline in Fig. 2d). It can be seen that, in the dual-task trials that presented the target stimulus, the controlled dot developed a lead over the lead dot in both the horizontal and vertical directions during the 600-800 and 800-1000 ms periods post stimulus-onset. Fig. 8 shows the spatial pattern of the lead and controlled dot's trajectories in the single-task motor, and dual-task target- and standard-stimulus conditions. The main figure shows that the controlled dot's trajectory deviates prominently in the dual-task, target-stimulus condition only. A magnified inset shows this deviation pattern in six representative participants.

FIGURE 8



Both the horizontal and vertical components of this deviation pattern were quantified using a 3 (task: motor-only single task, dual task with standard stimulus, dual task with target stimulus) x 6 (time: 0-200, 200-400, 400-600, 600-800, 800-1000, 1000-1200 ms) repeated measures ANOVA. In the case of horizontal deviation, the main effect of task was significant (F(2, 46) = 7.72, p<.001, η_G^2= .097), as was the main effect of time (F(6, 138) = 4.44, p<.001, η_G^2= .062). The interaction between task and time was also significant (F(12, 276) = 6.12, p<.001, η_G^2= .058). Comparison of means indicated that horizontal deviation in the dual-task target condition differed significantly from the other conditions in the 600-800 and 800-1000 ms time periods (see Fig. 2d). In the case of vertical deviation, the main effect of time (F(6, 138) = 3.18, p<.01, η_G^2= .041) and the interaction between task and time (F(12, 276) = 2.72, p<.01, η_G^2= .043) were significant. In post-hoc means comparisons, however, there were no significant differences between conditions in any of the time windows.

Relationship between P3b amplitude and visuomanual tracking deviation

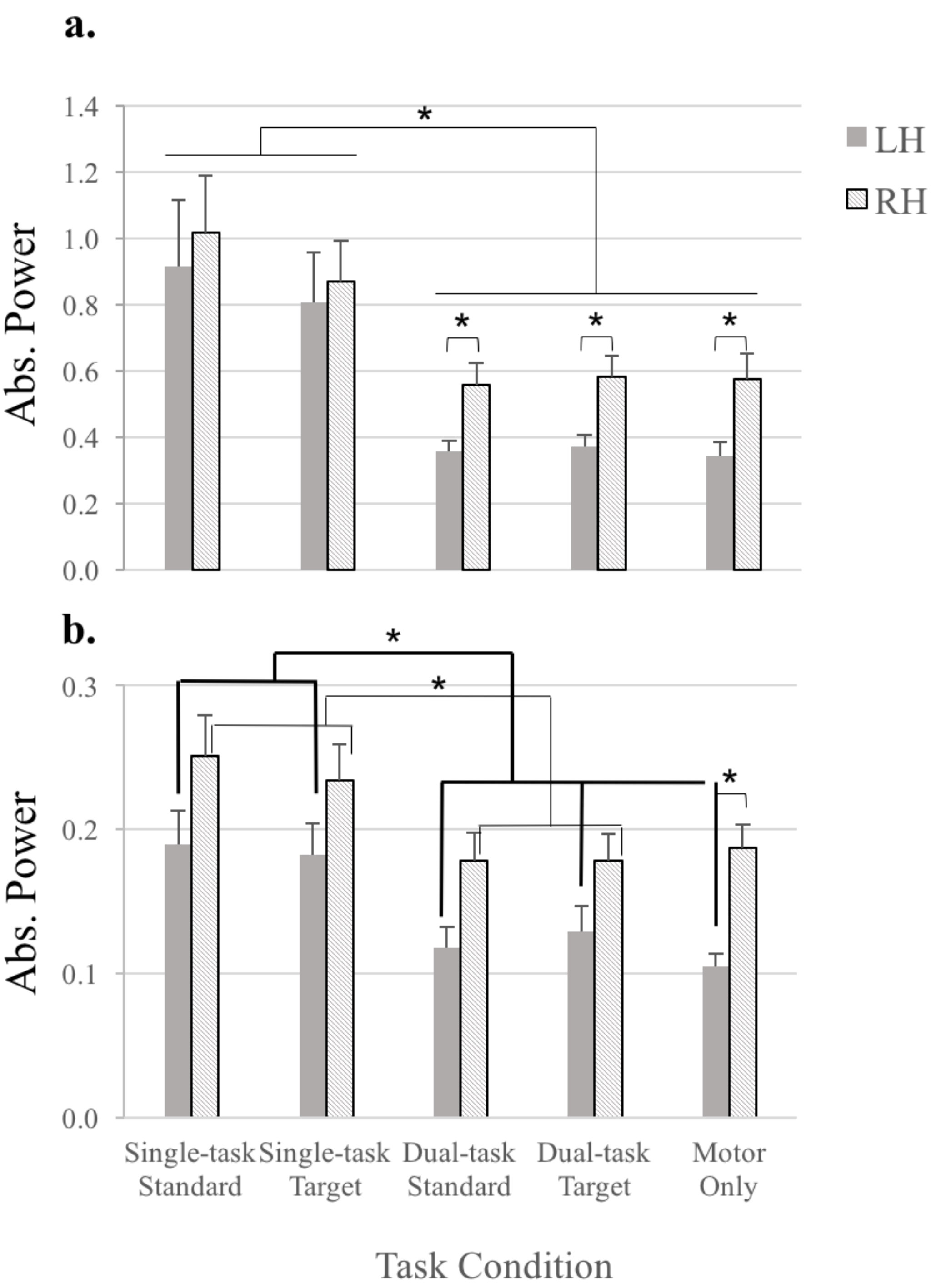
The dual-task target-stimulus condition produced a significant tracking deviation in the 500 ms time period following the P3b peak. As the P3b component corresponds to the recognition of the stimulus' task relevance, the observed trajectory deviation in fact occurred during the subsequent executive function of updating the target tally. To test whether tracking deviation may have been related to the P3b process, we correlated the P3b peak amplitudes with the maximum horizontal and vertical tracking deviations that followed. Neither horizontal (r = .126, p=.56) nor vertical (-.06, p=.77) deviation was significantly correlated with the P3b peak amplitude.

Effects of oddball task performance on spectral power over primary motor cortex

Visuomanual tracking occurred in three task conditions: motor-only, dual-task with the standard stimulus, and dual-task with the target stimulus. In these three conditions, we expected to observe event-related desynchronization (ERD) over motor cortex relative to the single-task standard and target oddball conditions (where there was no motor activity). Additionally, recall that if performing the oddball task while tracking reduced motor resourcing, we expected less ERD (more spectral power) in the two dual-task conditions relative to the motor-only condition. Separately for alpha and beta power bands, we conducted a 2 (hemisphere: LH, RH) x 5 (task: single-standard, single-target, dual-standard, dual-target, motor-only) repeated measures ANOVA using absolute power as the dependent measure (Fig. 9).

For the alpha band (Fig. 9a), the main effects of hemisphere ($F(1, 23) = 14.09$, $p<.001$, $\eta_G^2= .012$), and task ($F(4, 92) = 13.88$, $p<.001$, $\eta_G^2= .092$) were significant, but the interaction between hemisphere and task was not. For the beta band also (Fig. 9b), the main effects of hemisphere ($F(1, 23) = 13.98$, $p<.001$, $\eta_G^2= .012$), and task ($F(4, 92) = 19.29$, $p<.001$, $\eta_G^2= .084$) were significant, but the interaction between hemisphere and task was not. As Fig. 9 indicates, spectral power over motor cortex was reduced (i.e., ERD occurred) in the three task conditions involving tracking. Post-hoc mean comparisons did not find differences between the dual-task and motor-only conditions in either band, which suggests that motor programming resourcing was not impacted as a result of concurrently performing the oddball task.

FIGURE 9



In case any power differences occurred over shorter durations and therefore could not be detected over the whole trial period, we also analysed spectral power over left primary motor cortex (contralateral to the moving hand) using a 3(task: motor-only, dual-standard, dual-target) x 6 (time: 0-200, 200-400, 400-600, 600-800, 800-1000, and 1000-200 ms) repeated measures ANOVA. There were no significant effects, indicating that spectral power over motor cortex did not change across the motor-only and dual-task standard and target conditions.

Discussion

Performing the visual oddball task during visuomanual tracking reproduced performance deficits that are characteristic of dual-task interference. The participants made more errors in reporting the number of targets in the dual-task condition, and they also generated greater positional deviation in the tracking task, but only following the onset of target stimuli in the oddball task. Investigating these dual-task costs at the level of electrophysiological events generated significant new information, both about the possible selectivity of dual-task costs with respect to cognitive sub-processes, as well as asymmetry and asynchrony in reciprocal effects.

First, at around 100 ms, there was no dual-task effect on P1 component amplitude. Thus, there was no indication that tracking affected bottom-up perceptual processing of stimuli at this timescale. The stimulus effect (a larger P1 magnitude for the target stimulus which had greater contrast) under both single and dual task conditions also indicated that visual engagement in the tracking task did not compromise early-stage perceptual processing of the oddball stimulus. The P1 results suggest that the single and dual-task conditions were comparable in terms of participants’ ability to visually detect the oddball stimulus. Note that participants’ instructions throughout were to maintain eye-fixation at the center of the screen region where task stimuli appeared. So, eye movements, such as pursuit of the leading dot during tracking, played a minimal role, if any.

At 200 and 300 ms post stimulus-onset, dual-tasking did affect top-down categorization/template-matching (P2) and task-relevance judgement (P3b) processes. The P2 component is thought to signify top-down processes involved in comparing the current stimulus to representations of previous ones, such as the templates of standard and target stimuli in this oddball task (Kim et al. 2008; Luck 2005). The P3b is linked to the identification of the stimulus as a target, and hence its relevance to the response process (Polich 2007; Luck 2005). Attenuation of both component amplitudes during dual-tasking indicates that the resourcing of these top-down processes was compromised during concurrent performance of the tracking task.

The results of time-frequency analysis of EEG corroborated the ERP evidence of reduced resourcing of the oddball task during dual-tasking. The comparatively rarer encounter with the target stimulus is a change in processing that should instigate a parietal alpha-band ERD around 400-600 ms post stimulus-onset (Sutoh et al. 2000). During dual-tasking, we observed a significant reduction in this parietal ERD’s magnitude in the 450-650 ms time bin (Fig. 4, bottom-left panel), indicating that the neural process of target identification was not as robust as in the single-task situation. This result was also reflected behaviorally in reduced target-detection accuracy in the dual-task condition.

In addition to the above, concurrent performance of the tracking task was also found to affect the strength of the fronto-parietal network (Corbetta and Shulman 2002) that supports attention tasks such as oddball detection (Sauseng et al. 2006; Güntekin and Başar 2010; Sadaghiani et al. 2012; van Schouwenburg et al. 2017). The dual-tasking condition showed lower alpha-band magnitude and phase coherence between frontal and parietal networks, indicating that the large-scale cortical coordination that links bottom-up and top-down processes in attentional tasks was eroded when simultaneously performing the tracking task. We also observed increased frontal alpha-band power in the dual-task condition, which confirms that overall WM load increased while dual-tasking relative to the single task, as has also been observed in imaging studies of cognitive-motor dual-task interference (Holtzer et al. 2011; Doi et al. 2013; Meester et al. 2014; Leone et al. 2017).

These results show that concurrent visuomanual tracking had a negative impact on oddball task processes in the P2 and P3b time periods, suggesting that this type of CSC-cognitive dual-tasking reduces attentional resources available to the cognitive task. Reciprocally, however, no positional errors in tracking accumulated during these time periods. Performing the tracking task reduced the accuracy of oddball target detection, which could have resulted from interference in the P2-P3b timescale (where the waveforms were magnitude-attenuated when dual-tasking) or later during the executive function of updating the tally, or both (Fig. 1). In the reverse direction, the impact of oddball detection on tracking performance occurred only in the period after the P3b waveform, and then only in trials where the target stimulus was encountered. Moreover, the magnitude of tracking deviation was not correlated with that of the magnitude of the preceding P3b component. The fact that tracking deviation occurred only in the case of the target stimulus (which has also been observed previously see Gazes et al. 2010, for example), and that its magnitude was unrelated to that of the preceding P3b, together preclude the possibility that an earlier, more general interference resulted in delayed effects in the post-P3b response stages. Rather, the observed pattern strongly suggests that it was the cognitive response triggered by the target stimulus (i.e., the executive function of updating the target tally) that interfered with tracking. In this sense, the updating process could be considered a (cognitive) perturbation to the tracking coordination. Note that the tracking errors observed following target stimuli amounted to a phase advance relative to the lead stimulus (Fig. 2d), whereby the controlled cursor extended beyond the circle traced by the lead dot (Fig. 8). This pattern suggests that the perturbation, owning to the updating process in the target condition, did not affect the participants’ ability to generate hand motion per se, but rather impeded their ability to entrain the motion to the lead stimulus by keeping centripetal acceleration constant. In this respect, the pattern seen here differs from the pauses to tracking that were seen when postural perturbations were applied while visuomanual tracking was performed as a secondary task (McIlroy et al. 1999; Norrie et al. 2002). Previous research has also shown that reaction time to visual or auditory stimuli can be slowed when a perturbation is applied to a concurrent balancing function (e.g., Redfern et al. 2002). It is possible then, that the cognitive perturbation, owing to updating in the oddball task, slowed participants’ response to visual feedback of accumulating error while tracking on a circular path.

The interference pattern observed here shows that simply documenting reciprocal performance deficits at the behavioral level is not sufficient for understanding the micro-structure of interference between a CSC and a concurrent cognitive task. It is possible that, as in the present task combination, the CSC impacts the attentional components of the cognitive task, but it is an executive function component of the cognitive task that impacts the CSC. Also, these directional influences can occur at different times in the information-processing sequence. Such a finding was made possible in this study by the use of a multi-component cognitive task, and the deployment of neurophysiological methods to resolve interference effects to the specific time-scales of task components. The possibility or significance of such asymmetric and asynchronous CSC-cognitive interference has never been highlighted in the large and growing dual-tasking literature on everyday CSCs (e.g., driving, gait, or balancing). This is despite the fact that the vast majority of everyday cognitive tasks performed alongside common CSCs involve perception, attention, and executive functions, as well as a motor response in some cases.

Even using highly controlled laboratory tasks, it is rarely possible to arrange that the cognitive task only taps a single cognitive sub-process such as attention or EF. Everyday cognitive activities almost always combine a number of sub-processes. In addition, multiple simultaneous task demands activate executive attention processes that dynamically adjust cognitive resource allocation (Ridderinkhof, van den Wildenberg, Segalowitz, and Carter 2004). In the present study, performing the CSC alongside the oddball task evidently put pressure on available attentional resources, as indicated by attenuated P2, P3b, and parietal alpha-band ERD. However, this did not have a reciprocal effect on CSC performance in the same timescale. Thus, reduced resourcing of the cognitive task rather than the CSC was the preferred solution for dual-task demands at that timescale. This pattern is also seen in the context of whole-body CSCs such as gait or balancing, where priority is normally given to CSC maintenance at the expense of cognitive performance (e.g., the ‘posture-first’ principle) (Bloem et al 2001). Although, this strategy is stable for healthy young adults, in older people, particularly neurological patients, prioritization in the face of dual-task pressure does not always favour the CSC (Yogev-Seligmann et al. 2008). Parkinson’s (Bloem et al 2001) and stroke patients (Huitema et al. 2006) may prioritize the secondary task over gait or balancing, and even healthy older adults can prioritize their planning of future stepping at the risk of losing balance (Chapman and Hollands 2007). In this study, close inspection of the electrophysiological events associated with multiple cognitive sub-processes enabled the observation that CSC performance was maintained at the expense of resourcing the attentional component of the cognitive task in the 200-400 ms timescale, but this was not to achieve later at the timescale of the EF component of the oddball task.

As previously outlined, there is converging evidence that CSC stability is most consistently impacted by concurrent EF tasks. Even though CSC performance in the present study remained unperturbed as the oddball task's attentional sub-processes came under resourcing pressure, CSC errors did occur later during the EF sub-process of the same task. As the present task setting did not allow strategic adaptations (e.g., reducing CSC speed), or utilization of the kind of error tolerance that is inherent in everyday CSCs such as driving or walking, it provided strong evidence that concurrent demands for EF operations may be at the heart of CSC-cognitive interference. There is not a universally accepted list of the types of cognitive operations that comprise EF. In the context of CSC-cognitive dual-tasking, Yogev-Seligmann et al. (2008) identified volition (formulating goals, initiating action), self-awareness, planning (identifying and organizing sub-tasks), response-inhibition (disregarding irrelevant information), response-monitoring (detecting errors with respect to task goals) and attention allocation (distributing available cognitive resources among competing demands) as aspects of EF. An alternative to this functional approach has been to associate EF with specific operations performed on information held in WM. Miyake and colleagues (Miyake et al. 2000; Miyake and Friedman 2012) have proposed, for example, that EF involves updating (monitoring and altering WM contents), shifting (moving resources between task sets) and inhibition (suppressing effects of irrelevant information).

In terms of the latter approach, the EF component of the covert oddball task used in the present study was updating (the tally of target stimuli detected). CSC-cognitive dual-tasking have frequently addressed shifting (e.g., slowing down the CSC to accommodate cognitive operations) and inhibition (e.g., using Stroop tasks), but the effects of updating operations on a concurrent CSC's stability have not been highlighted. It might be that detecting the impact of updating was only made possible by severely curtailing the opportunity for shifting (by preventing speed variation). Updating task-relevant information in WM is patently ubiquitous in everyday cognitive activity. Indeed, shifting between task sets must also involve large-scale updating of which information is currently task-relevant, and even inhibition is only possible when the current task-relevance of information is kept updated. Even as updating processes are recognized as fundamental to performing or switching between cognitive tasks, it is worth noting that frequently updating the state is also fundamental to the maintenance of any CSC. This form of state-updating must integrate sensorimotor information on a grand scale, be tailored to the current task goals held in WM, and, importantly, maintain a high enough frequency to ensure CSC stability or counteract perturbations to it. It is highly plausible that pre-frontal cortex activity detected during CSCs, such as walking (Harada et al. 2009; Suzuki et al. 2004), is associated with state-updating. The extent to which updating operations can be performed simultaneously with respect to more than one task could be a key point in understanding CSC-cognitive interference, and indeed, dual-task interference more generally. It has been shown that just like CSC-cognitive dual-task performance, updating performance in EF tasks also declines with age (De Beni and Palladino 2004). Our results suggest that future research should focus on the possibility that the EF of updating is at the heart of CSC-cognitive interference.

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FIGURE CAPTIONS

FIGURE 1. (a) Dual-task arrangement. The oddball stimulus is either an unfilled (standard) or filled (target) circle in the centre of the screen. The tracking lead is the blue dot circling the oddball stimulus clockwise. The participant tracks the blue dot using a stylus on the digitizing tablet. Stylus position is displayed as a black dot on the screen. (b) Schematic representation of concurrent task demands (see text for details).

FIGURE 2. a-c: ERP difference waves derived from (a) right occipital, (b) fronto-central, (c) parietal electrode clusters, showing, respectively, P1, P2 and P3b waveform differences (target–standard, average referenced) in single and dual task conditions. Areas shaded in blue show statistically significant differences. No significant differences between single and dual-tasks were found for P1 (a). Both P2 and P3b show statistically significant differences between single and dual-task difference waves (b, c). The corresponding scalp topographies are of difference waves at 120, 200, and 400 ms post stimulus-onset. (d) Epoched tracking deviation (pixel difference between the controlled and leading dots) in the horizontal (top) and vertical (bottom) axes. The dotted vertical line at ~400ms indicates mean P3b peak latency. Both vertical and horizontal tracking deviation increased for dual-task target trials in the 600-800 ms and 800-1000 ms periods. Tracking results are shown separately for the oddball task's standard and target trials, and for the single-task condition in which participants only performed the tracking task.

FIGURE 3. (a) Mean P1, P2 and P3b ERP component amplitude differences (target-standard) for both single and dual task conditions. Both P2 and P3b difference wave amplitudes were

significantly attenuated in the dual-task condition. Error bars show standard errors.

FIGURE 4. Grand average time-frequency representation and fronto-parietal coherence of standard and target trials in single and dual task conditions. Left panels: spectral power changes (dB) as a function of time for standard (top) and target (bottom) trials at C21 (frontal) and A19 (parietal) electrodes; Right panels: event-related spectral coherence (ERSCoh) between C21 and A19 for standard (top) and target (bottom) trials. Parietal alpha desynchronization is shown for single-task target trials relative to dual-task target trials in the bottom two cells of the left panel. Frontal alpha synchronization for dual-task target trials relative to single-task can also be seen in the bottom left panel. Fronto-parietal alpha magnitude and phase coherence (right panel) can be seen to decrease during dual-task standard and dual-task target trials relative to single-task trials.

FIGURE 5. Mean parietal alpha power (dB) for standard and target trials in single and dual task conditions. (* Bonferroni-corrected significant difference). Parietal alpha power decreases for single-task target trials (alpha desynchronization) in the 500-700ms period relative to dual-task targets. Error bars show standard errors.

FIGURE 6: Mean frontal alpha power (dB) for both standard and target trials in single and dual task conditions at 10 time points from 550 to 1000 ms. Frontal alpha power increases for dual-task target trials (alpha synchronization) in the 650-750 ms period relative to single-task targets. Error bars show standard error.

FIGURE 7: Mean fronto-parietal magnitude (a) and phase (b) coherence for target stimuli in both single and dual task conditions at 20 time points from 50 to 1000 ms (* Bonferroni-

corrected significant difference). Fronto-parietal alpha magnitude and phase coherence are shown to be attenuated during dual-task target trials relative to single-task target trials. Error bars show standard errors.

FIGURE 8. Grand average epoched horizontal (X) and vertical (Y) deviation (pixels) in the manual tracking task. Stimulus onset time and mean P3b peak latency are marked by black lines crossing the time series. The insert shows a magnified view of X and Y deviation for dual-task target trials for six representative participants. In the target trials, the controlled dot's trajectory extended beyond the circular trace of the lead dot, indicating that participants were impeded in their ability to keep their motion entrained to that of the lead dot by maintaining a constant centripetal acceleration.

FIGURE 9. Alpha (a) and beta (b) band power over left and right primary motor cortex during all single and dual task conditions. Power was attenuated in the dual-task and motor-task only conditions, indicating desynchronization linked to motor activity. Desynchronization was greater in LH (the motor task used the right hand), but did not differ in either frequency band between the dual-task and motor task-only conditions. Error bars show standard errors.