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Research report

The unidirectional prosaccade switch-cost: Electroencephalographic evidence of task-set inertia in oculomotor control

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HIGHLIGHTS

- The completion of an antisaccade delays the RT of a subsequent prosaccade.
- It is proposed that this finding reflects task-set inertia in oculomotor control.
- Here we assessed the P3 ERP in an oculomotor task-switch experiment.
- P3 amplitude of task-switch prosaccades were comparable to antisaccade trial-types.
- The EEG finding support the proposal of task-set inertia in oculomotor control.

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ABSTRACT

The execution of an antisaccade selectively increases the reaction time (RT) of a subsequent prosaccade (the *unidirectional prosaccade switch-cost*). To explain this finding, the task-set inertia hypothesis asserts that an antisaccade requires a cognitively mediated non-standard task-set that persists inertially and delays the planning of a subsequent prosaccade. The present study sought to directly test the theoretical tenets of the task-set inertia hypothesis by examining the concurrent behavioural and the event-related brain potential (ERP) data associated with the unidirectional prosaccade switch-cost. Participants pseudo-randomly alternated between pro- and antisaccades while electroencephalography (EEG) data were recorded. As expected, the completion of an antisaccade selectively increased the RT of a subsequent prosaccade, whereas the converse switch did not influence RTs. Thus, the behavioural results demonstrated the unidirectional prosaccade switch-cost. In terms of the ERP findings, we observed a reliable change in the amplitude of the P3 – time-locked to task-instructions – when trials were switched from a prosaccade to an antisaccade; however, no reliable change was observed when switching from an antisaccade to a prosaccade. This is a salient finding because extensive work has shown that the P3 provides a neural index of the task-set required to execute a to-be-completed response. As such, results showing that prosaccades completed after antisaccades exhibited increased RTs in combination with a P3 amplitude comparable to antisaccades provides convergent evidence that the unidirectional prosaccade switch-cost is attributed to the persistent activation of a non-standard antisaccade task-set.

1. Introduction

The rapid reorientation of gaze towards a salient visual target (i.e., prosaccade) represents the most frequent motor response that humans perform on a day-to-day basis [29]. Notably, prosaccades require minimal top-down control due to their mediation via retinotopically organized motor maps within the superior colliculus ([46]; see also [39]). It is, however, possible to decouple direct stimulus and response (SR) relations and 'look' to any desired region of the visual field (i.e., non-standard task: see [17,32]). Indeed, non-standard tasks represent an important area of inquiry because they provide a framework for understanding how top-down cognitive control influences oculomotor networks. The antisaccade is an exemplar non-standard task and requires decoupling SR relations and the evocation of a saccade to a target's mirror-symmetrical location [24,25]. Extensive behavioural evidence has demonstrated that antisaccades have longer reaction times (RT) [24], increased directional errors [16,24], and less

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accurate and more variable endpoints [9,22,26] than prosaccades. These behavioural 'costs' have been attributed to the top-down suppression of a stimulus-driven prosaccade (i.e., response suppression) and the visual remapping (i.e., 180° spatial transformation) of the target's spatial location (i.e., vector inversion) ([20,47]; for review of the antisaccade task see [37]). Moreover, antisaccades have been linked to increased activity in an extensive fronto-parietal network (frontal eye field, supplementary eye field, dorsolateral prefrontal cortex, anterior cingulate cortex, and lateral intraparietal cortex) [5,8,11,18] and show a respective increase and decrease of collicular fixation and buildup neurons prior to target presentation [14,15]. The aforementioned changes to the oculomotor system are thought to reflect a preparatory response-set that withholds a reflexive prosaccade and permits sufficient time to complete the sensorimotor transformation necessary for an antisaccade [5].

In addition to the above-mentioned behavioural and neural changes linked to the antisaccade task, a series of recent studies have shown that the execution of an antisaccade lengthens the RT of a *subsequent* prosaccade ([6,7,10,41,42–45]). More specifically, results from our group have shown that the RT of a prosaccade completed after an antisaccade (i.e., task-switch prosaccade) are between 10 and 20 ms longer than a prosaccade completed after a prosaccade (i.e., task-repetition prosaccades). In contrast, RTs for task-switch and task-repetition antisaccades do not differ. As such, we have termed the selective increase in the RTs of task-switch prosaccades as the *unidirectional prosaccade switch-cost* and have shown that such an effect is not accounted for by the independent or interdependent effects of response suppression [44] and vector inversion ([45]; see also [10]). In accounting for the unidirectional prosaccade switch-cost our group extended [1] task-set inertia hypothesis to the oculomotor domain and proposed that responses entailing non-dominant SR mapping (e.g., an antisaccade) require the implementation of cognitively meditated task-rules (i.e., a task-set) for their successful execution. Moreover, the hypothesis asserts that the cognitively mediated task-set persists inertially and delays the planning of a subsequent response with standard and dominant SR mapping (e.g., a prosaccade). In turn, the hypothesis contends that the completion of a response with dominant SR relations does not require the activation of a cognitively based task-set and therefore does not influence the planning of a subsequent response with non-dominant SR mapping. Thus, task-set inertia asserts a null cost when switching from a prosaccade to an antisaccade.

An important issue to revolve is *how* a persistently active antisaccade task-set delays the planning of a subsequent prosaccade. In other words, identifying the component element of prosaccade planning that is influenced by the antisaccade task-set would provide a direct explanation of how the task-set inertia hypothesis accounts for the unidirectional prosaccade switch-cost. One possible explanation is shown in Fig. 1. In particular, the figure shows

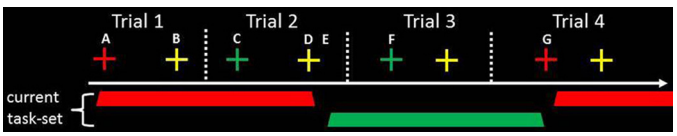

Fig. 1. Theoretical predictions for how task-set inertia elicits a unidirectional prosaccade switch-cost. Trials 1 through 4 represent task-repetition antisaccades (trial 1), task-switch prosaccades (trial 2), task-repetition prosaccades (trial 3) and task-switch antisaccades (trial 4). Red and green crosses denote anti- and prosaccade task-cues, respectively. Yellow crosses denote response-cuing (i.e., target presentation). Red and green rectangles at the bottom of the figure represent anti- and prosaccade task-sets, respectively. Notably, the figure shows that the task-cue for task-switch prosaccades (time C) is associated with an antisaccade task-set, whereas the task-cue for task-repetition prosaccades (time F) is associated with a task-set distinct from all other trial-types. That is, time F in the panel demonstrates a task-set with direct SR relations.

that advanced information specifying antisaccade task-cuing (time A) results in the adoption of a cognitively mediated antisaccade task-set in advance of the exogenous stimulus cuing the response (i.e., response-cuing; see time B). Importantly, the figure further shows that the antisaccade task-set persists inertially and is present throughout a subsequent prosaccade task- (time C) and response-cuing (time D) interval. Indeed, it is predicted that an appropriate prosaccade task-set is adopted only after response-cuing (time E) and it is only after this time that the ensuing response can be planned with standard SR rules. Put more simply, we propose that the basis for the prosaccade switch-cost is that the antisaccade task-set persists inertially and delays *when* the prosaccade task-set can be adopted. Furthermore, and as outlined in the preceding paragraph, Fig. 1 (time G) shows that the prosaccade task-set does not persist inertially and therefore does not delay the adoption of a non-standard antisaccade task-set.

Our explanation of the unidirectional prosaccade switch-costs is predicated on the assertion that the antisaccade task-set persists inertially and delays the adoption of the prosaccade task-set until after response-cuing. In other words, we propose that the preparatory interval (i.e., time between task-cuing and response-cuing) associated with task-switch prosaccades is associated with an antisaccade task-set, whereas the preparatory interval for task-repetition prosaccades is associated with its own distinct standard task-set (see Fig. 1). In order to test this hypothesis, the present investigation directly compared the concurrent behavioural and a human event-related brain potential (ERP) evoked by pro- and antisaccade task-switching. Notably, we identified the P3 ERP component as a means to measure the task-set inertia hypothesis because an extensive literature has shown that changes (i.e., modulation) in the amplitude of this waveform reflects the task-set required for a newly adopted response. For example, previous work in the motor control literature has shown that the amplitude of the P3–time-locked to task-cuing–differs between pro- and antipointing (i.e., the respective manual response analogues of pro- and antisaccades; [27]) and that the amplitude of the P3 is modulated when propointing must engage in an online trajectory correction to account for an unexpected target 'jump' [34]. More directly, the different P3 amplitudes for pro- and antipointing and for target jump and no-jump trials have been interpreted to reflect the task-set commensurate with current task-goals. Similarly, results from the perceptual literature have shown that task-switch and task-repetition trial-types are associated with distinct P3 amplitudes. For example, [21] demonstrated an increase in the amplitude of the P3 when participants switched from identifying the magnitude to the parity – or vice versa – of a to-be-presented numerical digit. According to the authors, the increase in P3 amplitude for task-switch trials reflected the adoption of the 'new' task-set required to successfully complete the response (see also [2,3,38]). Thus, convergent evidence indicates that modulation of the P3 reflect the adoption of a task-set required to meet the demands of the upcoming response.

In the current experiment participants initially viewed a task-irrelevant fixation cross and were then provided task instructions – via a fixation cross colour-change – which indicated whether to execute a pro- or antisaccade in response to an upcoming visual stimulus (i.e., task-cuing). The presentation of the target stimulus (i.e., response-cuing) occurred between 1000 and 2000 ms following the task-instruction cue. Importantly, we examined changes in P3 amplitude time-locked to, and evoked by, the task-instruction cue (i.e., the fixation cross colour-change) as this was the time-point when participants were informed whether to maintain or adopt a new task-set for the upcoming response. As such, the P3 time-locked to fixation cross colour-change provides an analogue of participants' premovement task-set. In terms of research predictions, if the unidirectional prosaccade switch-cost is explained

by the task-set inertia hypothesis then antisaccade trial-types (i.e., task-switch and task-repetition) and task-switch prosaccades should exhibit comparable P3 amplitudes. Indeed, such a finding would indicate that the increase in prosaccade RT following an antisaccade is due to the persistent activation of a task-set associated with non-standard SR rules. Moreover, it is predicted that task-repetition prosaccades will elicit a P3 amplitude that is different from the aforementioned trial-types–a result that would be consistent with the assertion that the preparatory interval for task-switch and task-repetition prosaccades are associated with non-standard and standard task-sets, respectively. Last, it is predicted that the P3 amplitudes of task-repetition prosaccades and task-switch antisaccades will reliable differ. Such a prediction is based on the task-set inertia hypothesis' assertion that the task-set associated with a response with dominant SR rules (i.e., a prosaccade) does not persist and delay the adoption of a task-set associated with non-standard SR rules (i.e., an antisaccade).

2. Methods

2.1. Participants

Fourteen individuals (11 females, 3 males; mean age 20.6 years, SD = 2.8) volunteered for the current investigation. All participants had normal or correct-to-normal vision and declared being right hand dominant. Prior to data collection participants provided informed written consent. This study was approved by the Office of Research Ethics, University of Western Ontario, and was conducted in accord with the guidelines of the Declaration of Helsinki.

2.2. Apparatus and procedure

Participants completed the experiment in an isolated testing suite while seated at a table with their head stabilized via a chin-rest. Visual stimuli were presented on a 22-inch LCD monitor (75 Hz, 2 ms response rate, 1680 by 1050 pixel, LG W2242TQ-GF, Seoul, South Korea) centred on the participant's midline at a viewing distance of 630 mm. The gaze location of the participant's left eye was obtained by a video-based desk-mounted eye-tracking system (Eye-Link 1000: SR Research, Ottawa, Ontario, Canada) sampling at 500 Hz. Prior to data collection a nine-point calibration of the participant's viewing space was completed and immediately validated. Outside the testing suite, the experimenter viewed two additional monitors that provided: (1) real-time point of gaze information, (2) a visual depiction of trial-to-trial saccade trajectories (e.g., displacement, velocity), and (3) information about the accuracy of the eye tracking system (i.e., to determine a necessary recalibration or drift correction). All computer events and visual stimuli were controlled via MATLAB (7.6: The Math Works, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0; [4]). The lights in the testing suite were extinguished during data collection.

Visual stimuli were presented against a high contrast black background and consisted of a fixation cross (1.0°) – appearing as white, green or red in colour (see details below) – that was centred horizontally on the monitor and at the eye-level of the participant. As well, yellow crosses (1.0°) served as target stimuli and were presented 12.5° left or right of the fixation cross and in the same horizontal meridian. Each trial began with the presentation of a task-irrelevant white fixation cross which alerted the participant to direct their gaze to its location. After a stable fixation was achieved (±1.5° for 500 ms) the white cross remained visible for an additional 1000 ms. To avoid anticipatory saccades, the white fixation cross was then replaced by either the green or the red fixation cross after a randomized foreperiod. The foreperiod was selected from a uniform distribution ranging from 1000 to 2000 ms. Following the foreperiod a target was briefly presented (i.e., 50 ms) and the fixation cross was simultaneously extinguished. The presentation of the target stimulus – and removal of the fixation cross – served as the response-cue to execute a required pro- or antisaccade (see details below). A 50 ms target presentation was used to eliminate between-task differences in retinal feedback following the completion of the saccade.

As mentioned above, the white fixation cross was task-irrelevant; however, the subsequent presentation of the green or red fixation cross denoted the participant's required response: The green fixation cross indicated a saccade to the target's veridical location (i.e., a prosaccade), whereas the red fixation cross indicated a saccade to the target's mirror-symmetrical location (i.e., an antisaccade). Pro- and antisaccades were presented in one of four pseudo-randomized task-switching schedules that were generated by the experimenter and could not be predicted by the participant (e.g., AABAABB. . .). All task-switching schedules contained 80 task-repetition (i.e., pro- or antisaccade preceded by its same task counterpart) and task-switch (i.e., prosaccade preceded by an antisaccade or vice versa) pro- and antisaccade trials resulting in 320 experimental trials. The visual field in which the target was presented was randomly selected on a trial-by-trial basis. As the first trial in the experiment was neither a task-repetition nor a task-switch trial, it was not included in subsequent analyses.

2.3. Electroencephalography (EEG) recording

Prior to data collection participants were fitted with a 64-electrode EEG cap. The electrodes were mounted in the standard 10–20 layout and were recorded using BrainVision PyCorder software (Version 1.0.4, Brainproducts GmbH, Munich, Germany) with a virtual ground built into the amplifier (reference-free acquisition). Electrooculograms were obtained by electrodes placed above and below the right eye and on the outer canthi of the left and right eyes. Electrical impedances for all electrodes were kept below 20 kΩ at all times. The EEG data was sampled at 500 Hz, amplified (ActiCHamp, Revision 2, Brainproducts GmbH, Munich, Germany) and filtered through an antialiasing low-pass filter of 8 kHz.

2.4. Data processing

Point of gaze data were filtered offline using a dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Filtered displacement data were used to compute instantaneous velocities via a five-point central finite difference algorithm. Acceleration data were computed similarly via the velocity data. Saccade onset was determined on the basis of velocity and acceleration values that exceeded 30°/s and 8000°/s^2, respectively. Saccade offset was marked when saccade velocity fell below 30°/s for 15 consecutive frames (i.e., 30 ms). Trials displaying an anticipatory response (i.e., RT < 70 ms), a delayed response (i.e., RT > 700 ms) or missing data (e.g., blinks) accounted for 5.3% of trials and were excluded from subsequent analysis.

For each participant the continuous EEG data were filtered offline through a phase shift-free Butterworth filter (0.1–20 Hz pass-band) and referenced to the two mastoid electrodes. Subsequent to this, 800 ms epochs of data (starting from 200 ms prior to fixation cross colour-change) were extracted from the continuous EEG signal for each trial and experimental condition (see above). Following the creation of epochs for all conditions, ocular artefacts were corrected via the algorithm described by [23]. Next, the final 200 ms of the task-irrelevant white fixation cross immediately preceding the conditional colour-change were used to baseline the EEG epochs. Finally, an artefact rejection algorithm discarded epochs wherein the change in voltage at any channel

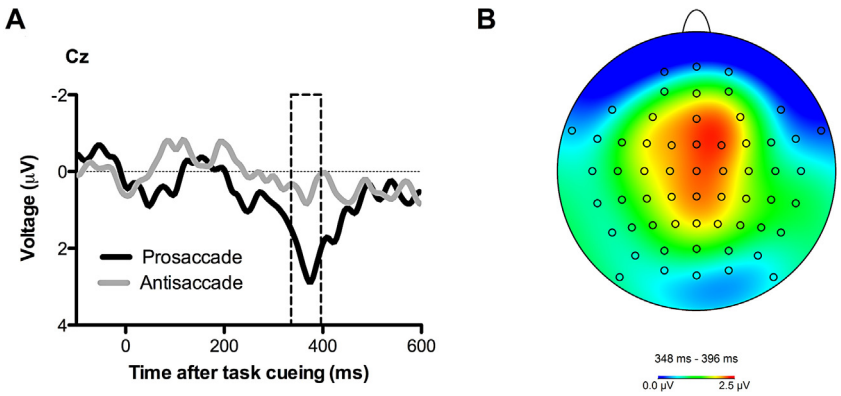

Fig. 2. (A) Difference waveforms computed by subtracting within task-type (task-repetition prosaccade minus task-switch prosaccade and task-repetition antisaccade minus task-switch antisaccade). The dashed line shows the window of analysis: 350–400 ms. (B) Scalp topography for the prosaccade difference waveform, maximal at electrode site Cz. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

exceeded 10 μV per millisecond or the change across the entire epoch (maxima–minima) was greater than 100 μV (2.3% of total trials).

ERP waveforms were created by averaging the epoched EEG data as a function of experimental condition (i.e., task-switch/task-repetition pro- and antisaccades) for each electrode channel and participant. In order to define the P3, we examined difference waveforms (as recommended by [36]) computed by subtracting within task-type (task-repetition prosaccade minus task-switch prosaccade and task-repetition antisaccade minus task-switch antisaccade). Based on previous literature [40] and on an examination of the within-task difference waveforms (Fig. 2a), the P3 was defined as the mean voltage 350 to 400 ms following the fixation cross colour-change on each of the conditional ERP waveforms. Our analysis focused on electrode channel Cz, where the prosaccade difference waveform was maximal (see Fig. 2b).

2.4.1. Dependent variables and statistical analysis

Dependent variables included mean RT (time between target onset and saccade onset), the number of directional errors (a saccade initiated and/or executed to the incorrect goal-location), the accuracy (i.e., signed error relative to veridical target location) and variability of saccade endpoints in the primary movement direction (i.e., horizontal), as well as P3 amplitude. Dependent variables were submitted to 2 (task: prosaccade, antisaccade) by 2 (task-transition: task-switch, task-repetition) repeated-measures ANOVA[1]. To determine whether there were task-specific switch-costs, reliable interactions were decomposed via within-task simple effects contrasts; that is, we compared: (1) task-switch prosaccades with task-repetition prosaccades, and (2) task-switch antisaccades with task-repetition antisaccades (see [31]). Results were considered reliably different at an alpha level of 0.05 or less, and Bonferroni adjustments were employed for post-hoc contrasts involving more than two means [2].

3. Results

3.1. Behavioural data

Analysis of RT yielded a main of task, $F(1,13) = 74.23$, $p = 0.000001$, $\eta^2_{partial} = 0.851$, task-transition, $F(1,13) = 9.72$, $p = 0.008$, $\eta^2_{partial} = 0.428$, and their interaction, $F(1,13) = 21.63$, $p = 0.0005$, $\eta^2_{partial} = 0.625$. Fig. 3 shows that prosaccade task-switch trials (227 ms, SD = 46) produced longer RTs than their task-repetition counterparts (206 ms, SD = 34), $t(13) = 4.33$, $p = 0.0008$, whereas antisaccade task-switch (289 ms, SD = 40) and task-repetitions (289 ms, SD = 34) trials did not reliably differ, $t(13) = 0.06$, $p = 0.952$.

Analysis of saccade directional errors yielded a main effect of task, $F(1,13) = 18.26$, $p = 0.0009$, $\eta^2_{partial} = 0.584$, and task-transition, $F(1,13) = 14.05$, $p = 0.002$, $\eta^2_{partial} = 0.519$. More directional errors were associated with antisaccades (7.0, SD = 4.75) than prosaccades (3.21, SD = 3.06), and more errors were associated with task-switch (6.71, SD = 4.61) than task-repetition (3.50, SD = 3.57) trials.

Analysis of saccade accuracy and variability yielded main effects of task, Fs(1,13) = 13.54 and 47.81, ps = 0.003 and 0.00001, $\eta^2_{partial} = 0.51$ and 0.79, respectively, for accuracy and variability. Prosaccade endpoints were more accurate (−0.8°, SD = 1.7) and less variable (1.7°, SD = 0.5) compared to antisaccades (accuracy: −2.4°, SD = 1.8; variability: 2.5°, SD = 0.6).

3.2. P3 amplitude time-locked to task-instruction

Analysis of the P3 amplitude yield main effects of task, $F(1,13) = 5.0$, $p = 0.043$, $\eta^2_{partial} = 0.28$, task-transition, $F(1,13) = 9.58$,

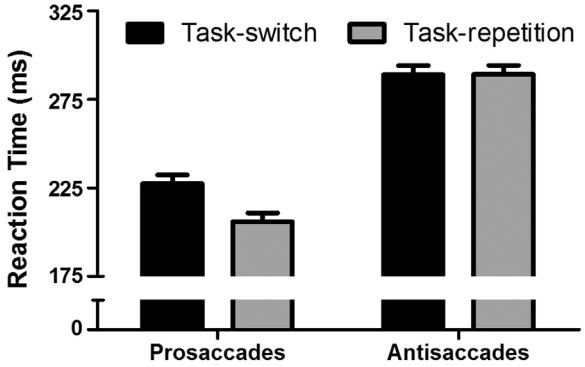

Fig. 3. Reaction time data for pro- and antisaccade as a function of task-switch and task-repetition trial-types. Results demonstrate the unidirectional prosaccade switch-cost. Error bars represent within-participant 95% confidence intervals [35].

[1] We included "trial schedule" as a between-participant factor in our initial ANOVA model. This variable did not elicit any significant main effects or higher-order interactions across each dependent variable (Fs < 1.10). As such, trial schedule was collapsed in the main analyses presented in the Results. Moreover, previous work has shown that task-ordering does not influence the unidirectional prosaccade switch-cost [42].

[2] The analysis of our EEG results required four post-hoc contrasts. As such, we used an alpha level of 0.0125 (i.e., Bonferroni correction) to denote reliable differences for our simple effects analysis.

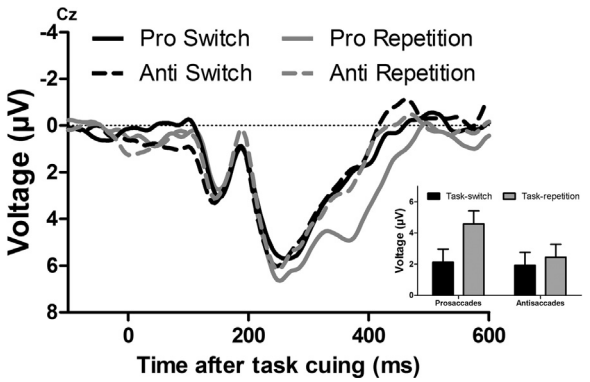

Fig. 4. Grand averaged waveforms – time-locked to task-cuing – for each of the four trial-types. Task-switch prosaccades as well as task-switch and task-repetition antisaccades exhibited comparable P3 amplitudes that were different from task-repetition prosaccades. The inset panel represents mean P3 amplitude for each of the four trial-types. Error bars on the inset panel represent within-participant 95% confidence intervals [35].

$p = 0.009$, $\eta^2_{partial} = 0.42$, and their interaction, $F(1,13) = 6.49$, $p = 0.024$, $\eta^2_{partial} = 0.33$. For prosaccades, P3 amplitudes differed between task-switch (2.13 μV, SD = 3.31) and task-repetition (4.59 μV, SD = 3.56), $t(13) = 4.05$, $p = 0.001$, trials, whereas antisaccade task-switch (1.94 μV, SD = 3.80) and task-repetition (2.44, SD = 3.74) trials did not reliably differ, $t(13) = -0.81$, $p = 0.43$. Moreover, and as outlined in the Introduction, our primary objective was to determine whether the unidirectional prosaccade switch-cost arises from an interially persistent non-standard task-set associated with a preceding antisaccade. In other words, we sought to determine whether the P3 amplitude associated with task-switch prosaccades was comparable to task-switch and task-repetition antisaccades. In addressing this issue we first note that the EEG waveforms shown in Fig. 4 qualitatively demonstrates that task-switch prosaccades as well as task-switch and task-repetition antisaccades produced comparable amplitudes at the P3 epoch and that these amplitudes differed from task-repetition prosaccades. Moreover, we addressed this issue quantitatively by contrasting the P3 amplitudes between: (1) task-repetition antisaccades and task-switch prosaccades and, (2) task-repetition prosaccades and task-switch antisaccades. The P3 amplitudes for task-repetition antisaccades and task-switch prosaccades did not reliably differ, $t(13) = 0.74$, $p = 0.48$, whereas a difference was observed between task-repetition prosaccades and task-switch antisaccades, $t(13) = 2.90$, $p = 0.010$.

4. Discussion

4.1. Pro- and antisaccade behaviour in oculomotor task-switching

The behavioural findings from this experiment were that antisaccades elicited longer RTs, more directional errors, and were associated with less accurate and more variable endpoints than their prosaccade counterparts. These results are in accord with an extensive literature and are taken as evidence that antisaccades require the top-down and time-consuming processes of response suppression and vector inversion (see [37]). Moreover, the present findings show that the completion of an antisaccade selectively delayed the RT of a subsequent prosaccade; that is, results demonstrate the unidirectional prosaccade switch-cost ([6,10,41–45]). As well, results showed that pro- and antisaccade endpoint accuracy and variability were not modulated across task-switch and task-repetition trials. Indeed, the results for saccade execution (i.e., endpoint accuracy and variability) are notable because they demonstrate that the unidirectional prosaccade switch-cost is limited to response planning.

4.2. Antisaccades delay the updating of SR relations: Electrophysiological evidence of a persistent task-set

The primary objective of this study was to test the task-set inertia hypothesis' contention that the prosaccade switch-cost results from a persistently active non-standard task-set. To address that issue, we measured the P3 amplitude across pro- and antisaccade task-switch and task-repetition trials. Notably, we time-locked our EEG data to a task-cuing stimulus (i.e., fixation cross colour-change) that provided participants with advanced information regarding the nature (i.e., pro- vs. antisaccade) of the to-be-completed trial (see also [2,3,38]). Fig. 4 shows that task-switch prosaccades as well as task-switch and task-repetition antisaccades elicited comparable P3 amplitudes, and that the former trial-types differed from task-repetition prosaccades. These results are notable for at least three reasons. First, the results show that the preparatory period (i.e., interval from task-cuing to response-cuing) of task-switch prosaccades was associated with the same underlying neural processes as that associated with task-switch and task-repetition antisaccades and was distinct from that associated with task-repetition prosaccades. Second, the ERP findings in combination with the selective increase in RT for task-switch prosaccades provides convergent support for the task-set inertia hypothesis' assertion that a prosaccade switch-cost arises from the persistent activation of a non-standard task-set. Third, the fact that task-repetition prosaccades produced a P3 amplitude that was distinct from task-switch antisaccades and that RTs for the latter task-type did not show evidence of a switch-cost further indicates that a task-set associated with a response with dominant SR mappings (e.g., a prosaccade) does not influence the adoption of the appropriate task-set for a subsequent response.

Three additional aspects of the EEG results should be addressed. First, recall that participants were provided a task-irrelevant white fixation cross and following a randomized foreperiod its colour was changed in order to provide task-relevant instructions (i.e., green = prosaccade; red = antisaccade). Notably, the EEG data were time-locked to the onset of the fixation cross colour-change. As such, it could be argued that the modulation of the P3 amplitude observed here reflects the fixation cross colour-change because the waveform has been shown to be sensitive to the presentation of novel or unexpected stimuli (i.e., *oddball effect*; for review see [19]). However, such an explanation is countered by the fact that each colour-change was unexpected given that pro- and antisaccades were pseudo-randomized and could not be predicted by the participants. Thus, our observation of a *selective* modulation of the P3 as a function of the saccade executed on the previous trial indicates that the results are due to task-set updating – or lack thereof – and not an oddball effect. Second, it should be noted that pro- and antisaccade task-instructions were restricted to the green and red fixation crosses, respectively. Thus, a potential limitation of the current work is that the behavioural and ERP findings relate to a task-specific processing of a specific fixation colour-change. Although we acknowledge this issue, it should be noted that previous work has shown that pro- and antisaccade RTs [9] as well as fMRI BOLD signals [5] are refractory to the colour cuing the response. Moreover, the ERP findings shown in Fig. 4 demonstrate that task-switch prosaccades yielded similar P3 amplitudes to task-switch and task-repetition antisaccades in spite of the fact that the tasks were elicited via separate fixation cross colour-changes. Third, we note that there was a reduction in the amplitude of the P3 for task-switch antisaccades relative to task-repetition prosaccades—a change in the waveform that we have attributed to the immediate adoption of an antisaccade task-set required to complete the upcoming trial.

Indeed, we raise this as an issue because some work in the cognitive task-switching literature has shown that 'switch' trials are associated with an increase in the amplitude of the P3 (e.g., [21]). Notably, however, results from the motor control literature indicate that the P3 amplitude is reduced for antipointing relative to propointing ([27]). Thus, in terms of goal-directed actions, the amplitude of the P3 may reflect the task-set that specifies the movement vector transformation (i.e., SR rules) that is to be implemented for the upcoming response.

4.3. The neural mechanism supporting an antisaccade task-set

The results observed here coalesce with previous work [44] in demonstrating that the prosaccade switch-cost is best explained by a persistently active antisaccade task-set. Thus, an important issue to address is the neural mechanism responsible for imparting the antisaccade task-set. A recent heterodox proposal by [13] asserts that the dorsolateral prefrontal cortex (PFC) provides excitatory input to the superior colliculus that "...is responsible for the encoding and implementation of task sets and task rules" (pg. 20130076)[3]. Such a proposal is based on non-human primate work showing that transient cooling of the PFC impairs in the animal's ability to maintain antisaccade task-rules in working memory [28] and eliminates the preparatory differences between pro- and antisaccades observed in the superior colliculus ([33]; see also [30]). Therefore, the prosaccade RT switch-cost may be the result of a sustained antisaccade task-set wherein the PFC continues to impart a respective increase and decrease in the activity of collicular fixation and saccade neurons ([15]; see also [14]).

5. Conclusion

We showed that the completion of an antisaccade selectively increased the RT of a subsequent prosaccade; that is, results demonstrated a unidirectional prosaccade switch-cost. Importantly, the P3 amplitude associated with task-switch prosaccades was comparable to task-switch and task-repetition antisaccades and the aforementioned trial-types were reliably different from task-repetition prosaccades. Thus, the concurrent behavioural and ERP findings suggest that the increased RTs of prosaccades task-switch trials relates to the persistent activation of a non-standard antisaccade task-set.

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