NeuroImage 45 (2009) 191–197

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

ERP indices of persisting and current inhibitory control: A study of saccadic task switching

S.C. Mueller [a,*], R. Swainson [b], G.M. Jackson [c]

[a] School of Psychology, University of Nottingham, UK
[b] School of Psychology, University of Aberdeen, UK
[c] Division of Psychiatry, University of Nottingham, UK

ARTICLE INFO

Article history:
Received 30 June 2008
Revised 29 October 2008
Accepted 12 November 2008
Available online 6 December 2008

Keywords:
Antisaccade
ERP
Cognitive control
Task switching
N2

ABSTRACT

Previous studies have found that inhibition of a biologically dominant prepotent response tendency is required during the execution of a less familiar, non-prepotent response. However, the lasting impact of this inhibition and the cognitive mechanisms to flexibly switch between prepotent and non-prepotent responses are poorly understood. We examined the neurophysiological (ERP) correlates of switching between prosaccade and antisaccade responses in 22 healthy volunteers. The behavioural data showed significant switch costs in terms of response latency for the prosaccade task only. These costs occurred exclusively in trials when preparation for the switch was limited to 300 ms, suggesting that inhibition of the prepotent prosaccade task either passively dissipated or was actively overcome during the longer 1000 ms preparation interval. In the neurophysiological data, a late frontal negativity (LFN) was visible during preparation for a switch to the prosaccade task that was absent when switching to the antisaccade task, which may reflect the overcoming of persisting inhibition. During task implementation both saccade types were associated with a late parietal positivity (LPP) for switch relative to repetition trials, possibly indicating attentional reorienting to the switched-to task, and visible only with short preparation intervals. When the prosaccade and antisaccade task were contrasted directly during task implementation, the antisaccade task exhibited increased stimulus-locked N2 and decreased P3 amplitudes indicative of active inhibition. The present findings indicate that neurophysiological markers of persisting and current inhibition can be revealed using a prosaccade/antisaccade-switching task.

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Introduction

The ability to control one's actions in accordance with internal goals is pivotal for human behaviour. However, how flexibly we can react to our environment depends on how familiar or biologically hard-wired any alternative, competing response is. The presence of competing responses requires that the cognitive control mechanisms allow both non-prepotent responses to be executed and prepotent responses to be re-enabled when necessary. This study examines the electrophysiological (ERP) indices of these mechanisms.

An extreme example of a hard-wired, prepotent response is a saccade. Saccades are ballistic eye movements, which are executed about 150,000 times a day (Schiller, 1998). In the laboratory, the tendency to execute an eye movement towards an object which abruptly appears (the prosaccade) is much stronger than the tendency to make an eye movement away from the object (the antisaccade; Hallett and Adams, 1980). It has been suggested that when an antisaccade is executed the prosaccade response is suppressed (for review see Munoz and Everling, 2004). Suppression of the prosaccade response on an antisaccade trial, however, may have a persisting negative effect on subsequent response latency (Fecteau and Munoz, 2003; Manoach et al., 2007).

A number of behavioural studies of non-saccadic tasks have examined the importance of task strength (i.e. task prepotency) on task switching performance. They have mainly demonstrated larger switch costs (increased reaction time or errors when the task switches relative to when it is repeated) for the stronger, prepotent task (Allport et al., 1994; MacLeod, 1991; Meuter and Allport, 1999). Arguably, during the execution of a weaker task, the stronger task has to be inhibited. This inhibition is thought to persist such that switching back to the stronger task requires the sustaining inhibition to be overcome, bringing a cost to the speed and/or accuracy of performance (e.g. Allport et al., 1994). A similar pattern of switch costs is observed for saccadic tasks when only a short period (200 ms) is available to prepare for a switch of task. Antisaccades, like the weaker task in the non-saccadic switching studies, show smaller latency switch costs relative to the cost associated with the switching to prosaccades (Barton et al., 2006). However, with longer preparation intervals a switch benefit for the antisaccade task has been observed (antisaccade switch latencies faster and errors lower than antisaccade repeat latencies and errors

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* Corresponding author. 15K North Drive, SDAN, MAP, NIMH, NIH, Bethesda, MD, 20892, USA. Fax: +1 301 402 2010.
E-mail address: msven@mail.nih.gov (S.C. Mueller).

1053-8119/$ – see front matter. Published by Elsevier Inc.
doi:10.1016/j.neuroimage.2008.11.019

(Barton et al., 2006; Reuter et al., 2006), and no switch costs for either task have also been reported (Hodgson et al., 2004).

An fMRI study of saccadic switching has highlighted a distinction between persisting and current inhibition (Manoach et al., 2007). During preparation for an antisaccade repeat trial, reduced BOLD activity in the frontal eye fields (FEF), supplementary eye fields (SEF) and parietal eye fields (PEF) was observed (relative to the antisaccade switch trial). In contrast, during preparation for a switch prosaccade trial (relative to repeat prosaccade), reduced activity was found only in SEF. These differences were interpreted in terms of maintaining suppression of the prosaccade response during preparation to repeat the antisaccade task, and dissipating suppression during preparation to switch to the prosaccade task. When prosaccades and antisaccades were compared directly, activity for antisaccades was increased in the FEF, possibly reflecting the current firing of afferent inhibitory neurones. Other studies have highlighted the crucial role of the SEF in the control of eye movements during such response conflict (Husain et al., 2003; Parton et al., 2007).

Similarly, electrophysiological recordings in the monkey have documented reduced FEF activity during preparation for antisaccades, (Everling and Munoz, 2000). Event-related potentials in humans (ERP) have characterised the sensorimotor transformation associated with shifting from a prosaccade to an antisaccade, and the inhibitory processes involved with the shift from a prosaccade to a NoGo response (Matthews et al., 2002), but not the switch to a prosaccade. A large number of recent studies have examined the ERP effects of switching between cognitive tasks during both task preparation and implementation stages, usually with manual responses and tasks which are symmetric, rather than asymmetric, in terms of overall difficulty (Mueller et al., 2007; Rushworth et al., 2002; Swainson et al., 2003). Enhanced late frontal negativities (LFN) have been reported during the later stages of task preparation that are modulated by whether tasks were changed or repeated. They are seen to vary depending on the response demands of the preceding trial as well as the extent to which responses are shared between tasks and may reflect processes associated with encountering inhibition of the switched-to task-set (Astle et al., 2006). ERP components associated with active inhibitory processes during the implementation phase are thought to be reflected in the N2/P3 complex (Jackson et al., 1999) possibly mirroring activations in prefrontal cortex and motor areas during go and no-go (i.e., inhibited) trials (Liddle et al., 2001). Finally, a switch-related enhanced late parietal positivity (affecting the later part of the P3 component, LPP) has been widely reported during both the preparation and implementation phases. The LPP component, however, is unlikely to reflect inhibition and instead may index attentional shifting (Astle et al., 2008b; Nicholson et al., 2005; Rushworth et al., 2002; Swainson et al., 2006).

We sought to characterise the temporal dynamics of the control mechanisms involved in switching between asymmetric tasks using dense-sensor ERPs and a mixed pro-/antisaccade task. Based on prior findings, we expected carry-over effects of the previous antisaccade to be visible in a sustained LFN specifically for switching to prosaccades but not antisaccades during saccade preparation (Astle et al., 2006, 2008a). We predicted that current inhibitory processes required for the implementation of antisaccades would be apparent in an increased N2 but decreased P3 components (relative to prosaccade) as previously seen for no-go responses (Jackson et al., 1999; Thorpe et al., 1996). It was also anticipated that a change in task would generate a late parietal positivity (LPP) that would be more increased for switch relative to repetition trials during either preparation or implementation and affecting both types of saccade (Rushworth et al., 2002; Swainson et al., 2003).

Materials and methods

Twenty-two neurologically healthy participants (9 males, mean age 22±2.6 years) with normal or corrected-to-normal vision participated in the study. All participants were right-handed (Edinburgh Handedness Inventory, (Oldfield, 1971) and received £10. Ethical guidelines of the University of Nottingham were followed and participants provided written consent. One participant had to be excluded from analysis due to excessive artefacts in the EEG.

Stimuli were projected onto a white wall in a dimly lit room 1.7 m away from the subject. A coloured cue (red or green) consisting of a fixation cross (2.4°) was presented in the centre of the screen on a black background. The cue was presented for one of two cue-to-target intervals (CTIs, 300 ms or 1000 ms), randomised from trial to trial: while the long CTI would allow us to observe ERP effects of preparation prior to target onset, the short CTI would encourage speedy preparation on all trials and allow us to examine the extent to which subjects prepared for a change in task (shown by the reduction in switch cost from short to long CTI). The white target box (1.85°) then appeared on either the left or the right hand side of the fixation cross (15°) and was displayed for 700 ms. Participants were instructed to make an eye movement towards the target box when the fixation cross (cue) was green (prosaccade trial) and an eye movement away from the target box equidistant into the opposite direction when the fixation cross was red (antisaccade trial). They were instructed to hold their fixation there until the target box disappeared and then return to the central fixation cross. The interval between the disappearance of a target stimulus and the appearance of the next cue was jittered between 2000 and 2400 ms in 100 ms increments in order to avoid anticipation of cue onset. To achieve equal trial durations across trial types, on trials with a 300 ms CTI an additional 700 ms passed before presentation of the next cue.

The experiment consisted of two parts. A single task and a mixed task block were recorded, the order of which was counterbalanced. However, only the data from the mixed blocks will be presented here given that the primary focus of this study lay on trial transitions. The mixed block consisted of 180 experimental trials with prosaccades and antisaccades being randomised from trial to trial. Because the saccade type (prosaccade or antisaccade) was selected at random on each trial, mixed blocks included equal numbers of ‘switch' (where the current saccade type differs from that on the previous trial) and ‘repetition' trials (where the previous saccade type is repeated on the current trial). Consequently, switch versus repetition trials comprise the ‘transition' factor. The block was repeated twice to give participants the opportunity to have a break in between.

Procedure

Analysis

Behavioural data

For analysis of the behavioural data (response latency and error percentage), a 2×2×2 repeated-measures ANOVA was conducted with the factors of transition (switch vs. repetition), CTI (300 vs. 1000) and saccade task (prosaccade vs. antisaccade). Planned comparisons were made to correspond to the ERP analyses and therefore examined the effects of transition within each saccade type and CTI, as well as the effects of saccade type at each CTI (collapsed across saccade type). For each subject, the first four trials were considered practice and removed from analysis.

ERP data

The horizontal electrodes that are usually used for monitoring eye movements of the EEG net (HEOG, EGI sensors 125 and 128) were used to retrieve the latency and accuracy data, and saccades were scored manually offline using Matlab (Mathworks, Natick, MA). In order to increase the signal-to-noise ratio of the EEG data for the scoring of the behavioural data only, a Chebychev 2 filter was applied in addition to a standard noise filter for EEG data. The filter was arrived