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Electrophysiological evidence for the involvement of proactive and reactive control in a rewarded stop-signal task

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ABSTRACT

Reward availability is known to facilitate various cognitive operations, which is usually studied in cue-based paradigms that allow for enhanced preparation in reward-related trials. However, recent research using tasks that signal reward availability via task-relevant stimuli suggests that reward can also rapidly promote performance independent of global strategic preparation. Notably, this effect was also observed in a reward-related stop-signal task, in which behavioral measures of inhibition speed were found to be shorter in trials signaling reward. Corresponding fMRI results implied that this effect relies on boosted reactive control as indicated by increased activity in the 'inhibition-related network' in the reward-related condition. Here, we used EEG to better characterize transient modulations of attentional processes likely preceding this ultimate implementation of response inhibition. Importantly, such modulations would probably reflect enhanced proactive control in the form of more top-down attention to reward-related features. Counter to the notion that behavioral benefits would rely purely on reactive control, we found increased stop-evoked attentional processing (larger N1 component) on reward-related trials. This effect was accompanied by enhanced frontal P3 amplitudes reflecting successful stopping, and earlier and larger ERP differences between successful and failed stop trials in the reward-related condition. Finally, more global proactive control processes in the form of a reward context modulation of reward-unrelated trials did not have an effect on stopping performance but did influence attentional processing of go stimuli. Together, these results suggest that proactive and reactive processes can interact to bring about stimulus-specific reward benefits when the task precludes differential global preparation.

Introduction

In everyday life it is important to adapt behavior to changing situational demands, a function that has been broadly labeled cognitive control. A central component thereof is the ability to rapidly withhold an already-initiated motor action when needed. This inhibition process has been investigated frequently using the stop-signal task, in which responses to a go stimulus occasionally have to be canceled upon the rapidly following presentation of a stop signal (Logan, 1994; Logan and Cowan, 1984). The processes underlying this task are usually explained by the well-validated horse-race model which assumes that the behavioral outcome (successful or unsuccessful stopping) is determined by a race between a go and a stop process, which are largely independent (Logan and Cowan, 1984, see also Boucher et al., 2007). Based on this model a measure for the duration of the implementation of response inhibition can be derived, the so-called stop-signal response time (SSRT), which has been shown to be prolonged in several neuropsychiatric disorders such as attention-deficit hyperactivity disorder, obsessive-compulsivity disorder and schizophrenia (Bekker et al., 2005c; Chamberlain et al., 2006; Lijffijt et al., 2005; Lipszyc and Schachar, 2010).

While different cognitive functions, including cognitive control, are usually studied in settings devoid of explicit extrinsic motivation, it has been shown that reward prospect can have beneficial effects on a range of cognitive functions like working memory (Beck et al., 2010; Gilbert and Fiez, 2004), memory formation (Adcock et al., 2006), and attention (Krebs et al., 2009; Padmala and Pessoa, 2011; Schevernels et al., 2014; Stoppel et al., 2011). In these studies, motivation is usually implemented using a cue indicating that a reward can be obtained if the upcoming task is performed correctly (monetary incentive delay task;

Abbreviations: CSDs, current source densities; EEG, electroencephalography; ERP, event-related potential; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; rANOVA, repeated-measures analysis of variance; RT, reaction time; SN, selection negativity; SSRT, stop-signal reaction time; SST, successful stop trial; UST, unsuccessful stop trial.

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Knutson et al., 2000). Hence, reward effects have usually been investigated with respect to preparatory proactive processes showing that reward prospect improves behavioral performance largely via enhanced top-down preparatory control (Chelazzi et al., 2013; Pessoa and Engelmann, 2010). The few studies that have looked at reward effects on response inhibition thus far have used such task contexts that allow for differential preparation by implementing cues indicating reward availability (e.g., Greenhouse and Wessel, 2013; Rosell-Negre et al., 2014; Scheres et al., 2001). Breaking with this traditional setup, we have recently shown that reward can also influence response inhibition without the involvement of global preparatory functions (Boehler et al., 2012b, 2014, but see also Wilbertz et al., 2014). Instead of pre-cueing reward prospect, the color of the stop signal itself indicated whether successful stopping would be rewarded. Despite the fact that participants could not globally prepare for rewarded trials in advance, response inhibition was facilitated (shorter SSRTs) for reward-related trials. Moreover, functional magnetic resonance imaging (fMRI) results suggested that this behavioral benefit was due to enhanced reactive control mechanisms as indicated by reward-related enhancements in right-lateralized medial and lateral prefrontal brain regions that are considered to be central to response inhibition in general (Boehler et al., 2014).

Yet, it is possible that this enhanced control was not completely independent of additional proactive processes. Specifically, although global proactive control enhancements were precluded because reward-related trials were unpredictable, stimulus-specific proactive control could still have been involved if observers strategically screened for the reward-related color. This may have increased the sensory response to the reward-related stop signal. Given the tight timing of different processing stages in this task, it is quite possible that fMRI would not be sensitive to transient changes in attentional processes. Here, methods with higher temporal resolution like electroencephalography (EEG) or magnetoencephalography (MEG) might be more suitable, and have in fact already been used to establish a general role of attentional processes in the dynamics of the processes underlying the stop-signal task. Specifically, it has been demonstrated that the size of the sensory stop signal-locked N1 component is related to ultimate stopping success, with larger N1 amplitude being found for successful stop trials (Bekker et al., 2005a; Boehler et al., 2009). This effect likely indicates that more attention was devoted to the stop-stimulus, possibly at the cost of paying less attention to the preceding go-stimulus, and that the distribution of attentional resources is likely under active top-down control (Boehler et al., 2009). In line with this notion, in a recent study of Greenhouse and Wessel (2013) that implemented a paradigm in which cues indicated the relative value of stopping and going, it was observed that the N1 component was enhanced when cues emphasized stopping over going. In this case N1 amplitudes were enhanced for successful and unsuccessful stop trials implying a generally enhanced deployment of top-down visual attention to the stop signal in this condition. Hence, in the current study we implemented our previous rewarded stop-signal paradigm (Boehler et al., 2012b, 2014) in an EEG setting to be able to identify transient modulations of attention that might precede the implementation of response inhibition. More specifically, we expected an enhanced stop-locked N1 component in successful stop trials in line with previous studies (Bekker et al., 2005a; Boehler et al., 2009). Furthermore, if the current event-related reward manipulation induced changes in proactive attentional control (in the form of enhanced top-down attention) we expected larger stop-evoked N1 amplitudes in stop trials that signal reward availability.

Besides the possible role of stimulus-specific attentional control, global preparatory control processes could still generally occur in our task. Specifically, even though our task equates such processes between reward-related and reward-unrelated trials, global preparation can play a role in the form of a general context effect in the current task. For example, Jimura et al. (2010) showed that when reward-unrelated trials were intermixed with reward-related trials (which triggered a proactive control mode), working memory improved also for reward-unrelated trials. Moreover, other studies have shown that behavioral measures for cognitive functions, like conflict adaptation (Braem et al., 2012) and action-effect binding (Muhle-Karbe and Krebs, 2012), can be altered for reward-unrelated trials in a rewarded context. These results suggest that a reward context can create a global state of sustained strategic proactive control (see also Locke and Braver, 2008). In order to investigate whether such global processes also occur in our task and whether they influence response inhibition, in the present study we added a control block in which none of the trials were associated with reward. Behaviorally this context effect should show up when comparing inhibition-related parameters, in particular the SSRT, in no-reward trials from the no-reward block with no-reward trials from the reward block. Specifically, if the reward-unrelated trials in the reward block would benefit from being in a rewarded task context, we should also find improved behavioral performance in these trials (compared to trials in the no-reward block). Given that the introduction of different contexts or blocks can create changes in the sustained attentional state that might affect the processing of all stimuli including go signals, we also explored the early attention-related go-locked N1, which has been related to strategic deployment of visual attention to the go stimulus (Boehler et al., 2009).

In addition to the specific interest in attentional components possibly reflecting proactive control, EEG offers a rich view on the process dynamics in the stop-signal task, allowing us to also study possible modulations of later, presumably control-related, components in relation to the reward availability and context manipulation. Most studies using event-related potentials (ERPs) in the stop-signal and go/no-go task, have focused on the frontal N2 and P3, labeled the N2/P3 complex (e.g. Bekker et al., 2005a; Bokura et al., 2001; Eimer, 1993; Huster et al., 2010, 2011; Kok et al., 2004; Ramautar et al., 2006a; Schmajuk et al., 2006; van Boxtel et al., 2001; van Gaal et al., 2011). Recent studies have found that the N2 is usually larger in unsuccessful than in successful stop trials suggesting a general role in response control, conflict monitoring and error processing (Dimoska et al., 2006; Enriquez-Geppert et al., 2010; Greenhouse and Wessel, 2013; Huster et al., 2013). In contrast, particularly the frontal P3 has been argued to reflect actual reactive inhibition in the stop-signal task (e.g. Bekker et al., 2005a; Dimoska et al., 2006; Enriquez-Geppert et al., 2010; Lansbergen et al., 2007). Thus, in line with these previous studies, we expected larger N2 amplitudes in unsuccessful stop trials and larger P3 amplitudes in successful stop trials (e.g. Dimoska et al., 2006; Greenhouse and Wessel, 2013; Senderecka et al., 2012). Moreover, concerning reward modulations, the aforementioned study by Greenhouse and Wessel (2013) showed that the frontal stop-evoked P3 was larger when stopping was successful compared to unsuccessful, and that this difference was larger when stopping was rewarded over going. Hence, boosted reactive control in reward-related stop trials, as indicated by our previous fMRI study (Boehler et al., 2014), might be mainly reflected by modulations of the stop P3 component. Also previous studies have observed earlier peak latencies for the N2 and P3 components (Kok et al., 2004) and earlier onsets of the P3 (Wessel and Aron, 2015) in successful compared to failed stop trials, suggesting that an earlier implementation of the internal response to the stop signal increases the likelihood of successful stopping. Therefore, reward-related differences in reactive response inhibition could also entail latency differences of the successful and unsuccessful stop-related N2 and P3. Hence, the overall aim of the current study was to investigate reactive control processes that have been shown to be susceptible to reward manipulations in a broader mechanistic context which includes a possible role of transient and sustained attentional processes.

Materials and methods

Participants

Twenty healthy right-handed students were recruited for the experiment (6 males, mean age = 22 years, range = 18–26 years). Subjects