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The neurophysiological basis of reward effects on backward inhibition processes

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ABSTRACT

The ability to flexibly switch between tasks is an important faculty in daily life. One process that has been suggested to be an important aspect of flexible task switching is the inhibition of a recently performed task. This is called backward inhibition. Several studies suggest that task switching performance can be enhanced by rewards. However, it is less clear in how far backward inhibition mechanisms are also affected by rewards, especially when it comes to the neuronal mechanisms underlying reward-related modulations of backward inhibition. We therefore investigated this using a system neurophysiological approach combining EEG recordings with source localization techniques. We demonstrate that rewards reduce the strength of backward inhibition processes. The neurophysiological data shows that these reward-related effects emerge from response and/or conflict monitoring processes within medial frontal cortical structures. Upstream processes of perceptual gating and attentional selection, as well as downstream processes of context updating and stimulus-response mapping are not modulated by reward, even though they also play a role in backward inhibition effects.

Introduction

In many daily situations we are required to switch between different tasks. Yet, this switching goes along with performance costs, i.e. slower responses and higher error rates. For successful task switching, both an efficient activation of a new task and an inhibition of the no longer relevant previous task are important (Allport et al., 1994; Jamadar et al., 2010; Mayr and Keele, 2000). The process that inhibits the most recently performed task upon switching to a new one is referred to as backward inhibition (BI), and serves the suppression of interferences arising from previous tasks (Allport et al., 1994; Allport and Wylie, 1999; Costa and Friedrich, 2012; Mayr and Keele, 2000). A stronger BI is thought to be related to a better task-switching performance, as it facilitates the activation of a new task set (Mayr and Keele, 2000). However, a strong BI can also be disadvantageous, since the inhibition of a currently irrelevant task can persist over time making it difficult to perform a previously inhibited task when it becomes relevant again (Allport et al., 1994; Allport and Wylie, 1999). To examine these processes, experimental paradigms assessing the time costs of overcoming the inhibition of a recently abandoned task set which becomes relevant again have been developed to measure task set inhibition (Mayr and Keele, 2000). Performance costs related to BI are observed in task sequences in which a task A is repeated from n-2 trials (e.g. ABA task triplet/BI condition), compared to when that task A has no n-2 trial sequence history (e.g. CBA task triplet/non-BI condition).

Executive control functions are generally known to be modulated by reward manipulations and it has been shown that rewards improve performance in many kinds of cognitive control tasks (Braem et al., 2012; Libera and Chelazzi, 2006; Veling and Aarts, 2010). In this context, Notebaert and Braem (2015) proposed that different reward components are associated with different kinds of cognitive control behavior: While the hedonic aspect of reward promotes explorative behavior and flexibility, the learning component of reward induces exploitative behavior increasing stability, and the motivational component of reward promotes anticipatory behavior (Notebaert and Braem, 2015). With regard to task switching, some studies showed that reward can reduce the switch costs (Kleinsorge and Rinkenauer, 2012; Savine et al., 2010; Shen and Chun, 2010). As BI is central to the "magnitude" of emerging switch costs, it seems that BI effects should be modulated by rewards as well. Yet, evidence for this assumption is sparse: Jiang and Xu (2014) reported that reward modulates inhibitory processes underlying task switching but they do not provide insights into the underlying neurophysiological mechanisms and functional neuroanatomical structures. In the current study, we combine EEG (event-related

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potentials, ERPs) with source localization techniques (i.e., sLORETA) to answer the question which neurophysiological processes within the processing cascade from early attentional processes to response selection mechanisms are changed in timing or intensity by reward modulation of the BI effect and what functional neuroanatomical networks are involved. In this context, it needs however to be mentioned that we used a between-subject manipulation with two different group conditions (i.e. performance-based reward for every trial vs. no reward for any trial) whereas the reward schedule of Jiang and Xu, randomly rewarded one third of their trials indicating reward trials with an additional monetary symbol (Jiang and Xu, 2014), With respect to the theory by Notebaert and Braem (2015), we investigated the effects of motivation/reward anticipation while Jiang and Xu investigated the effects of reinforcement history. It is known that reward modulates conflict monitoring and response selection processes (Braem et al., 2012; Krebs et al., 2013). Compared to the non-BI condition (CBA), the reactivation of the recently abandoned task intensifies response selection and conflict monitoring processes and causes a conflict indicating the need for additional allocation of control in the BI condition (ABA). However, the exertion of this control is assumed to carry an inherent subjective cost. As a consequence, the exertion of cognitive control depends on the expected value of control. In other words, the allocation of control is driven by a cost-benefit analysis which is likely to be modulated by rewards (Shenhav et al., 2013). Based thereon, we expect that rewards affect the BI and non-BI condition differently. Inasmuch as the N2 component has been demonstrated to reflect cognitive control and conflict monitoring processes (Botvinick et al., 2004; Deng et al., 2015; Donkers and van Boxtel, 2004; Folstein and Van Petten, 2008; Huster et al., 2013; Larson et al., 2014), we expect that the N2 component shows relevant differences related to the reward modulation of the BI effect. The anterior cingulate cortex (ACC) is highly associated with conflict-related N2 (Folstein and Van Petten, 2008; Yeung and Cohen, 2006). It plays an important role in conflict monitoring and in assessing the need for cognitive control (Botvinick et al., 2004; Cavanagh and Frank, 2014; Folstein and Van Petten, 2008; Holroyd and McClure, 2015; Kerns et al., 2004; Shenhav et al., 2013). Hence, reward-related modulations of the BI effect should be associated with the ACC. Yet, reward is supposed to have effects on attentional processes as well: It has been shown that the N1 and P2 components are modulated by reward, suggesting changes in attentional processes and the distinctive allocation of attentional resources (Chmielewski et al., 2015; Doñamayor et al., 2012; Flores et al., 2015; Stock et al., 2015; Sugimoto and Katayama, 2013; Yu and Zhou, 2006). Based thereon, it is possible that attentional selection processes during backward inhibition are also modulated by rewards. Matching this, the N1, which is known to reflect attentional selection processes (Beste et al., 2010; Gajewski et al., 2013; Herrmann and Knight, 2001; Luck et al., 1990; Wascher and Beste, 2010), has been demonstrated to be larger in the BI condition than in the control condition (Sinai et al., 2007). This suggests that attentional selection processes in the BI condition are intensified to re-activate the recently abandoned task, which makes it possible that these mechanisms are also modulated by rewards. Given that dopaminergic innervation, which also carries reward signals (e.g. Schultz, 1998), is less strong in occipital and parietal areas than in medial frontal (ACC) regions (Nieoullon, 2002), it is however possible that attentional processes show less reward modulation effects than response selection and conflict monitoring processes.

Another process which could be involved in backward inhibition is reflected by the P3 ERP. During task switching, the P3 has been linked to processes of context-updating and stimulus-response re-mapping (e.g. Finke et al., 2012; Gajewski and Falkenstein, 2011; Polich, 2007). Given that the BI effect arises in the situation, where a recently abandoned task becomes relevant again, it is possible that the BI effect relates to difficulties in context-updating and the decision of stimulus-response mapping, which can be reflected in the P3. Some studies found that the P3 components are also modulated by the reward, which has been ascribed to the increased attention to reward predictive cues (Krebs et al., 2013) and the updating of the internal environment (Broyd et al., 2012; Flores et al., 2015; Gruber and Otten, 2010). On these grounds, we expected that reward modulation might be shown in the P3 components.

Materials and methods

Participants

N = 56 healthy subjects between 18 and 30 years of age took part in the experiment. Participants were allocated to a control group (mean age of 23.7 ± 3.3; 18 females, 10 males) and a reward group (mean age of 23.6 ± 3.2; 18 females, 10 males) which were matched for sex and age. All participants were right-handed, had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. Written informed consent was obtained from all participants at the beginning of the experiment. The study was approved by the institutional review board of the Medical faculty of the TU Dresden in Germany and conducted in accordance with the declaration of Helsinki.

Task

We used a modified version of the backward inhibition paradigm proposed by Koch et al. (2004) to examine the influence of reward on the BI effect (see also: Zhang et al., 2016). A square, diamond, or triangle frame were used as cues, indicating task A (odd/even), task B (smaller/larger), or task D (double-press), respectively. Target stimuli consisted of digits 1–9 except for 5. Each trial started with the presentation of one of the cues. After a stimulus onset asynchrony (SOA) of 100 ms, a target occurred within the cue frame. Both stayed on the screen until the participants responded. In the odd/even task, participants should indicate whether the target digit was odd (left index finger press) or even (right index finger press). In the smaller/larger task, they should indicate whether the target was smaller (left index finger) or larger (right index finger) than five. In contrast to that, participants should press both buttons simultaneously (with an asynchrony of less than 50 ms) upon target presentation in the double-press task. Responses were given on the two Ctrl-buttons of a custom keyboard. If participants did not respond within 1000 ms after target onset, a speed-up sign (German Word “Schneller!”, translating to “Faster!”) appeared above the cue asking participants to respond more quickly. Between trials, there was a fixed 1500 ms response-stimulus interval (RSI), during which a fixation cross was centrally presented. In case of a slow (more than 1000 ms in the task D, 2500 ms in tasks A and B) and/or erroneous response, the German feedback “zu langsam!” (translating to “too late!”) and/or “falsch!” (translating to “wrong!”) was centrally presented during the first 500 ms of the RSI (as shown in Fig. 1). Incorrect key presses, too slow responses and non-simultaneous key-presses in the double-press task were counted as errors.

The experiment consisted of 768 trials divided into 8 equally sized blocks. Each cue and target as well as each possible combination of them were randomized and occurred with the same frequency. However, neither cues nor target could be the same in two consecutive trials. Furthermore, the target in the current trial was always different from the target used in the last trial with the same cue. Within each block, each trial (except for the first two trials, of course) built a triplet with the last two preceding trials. Hence, there was a total of 752 triplets. All twelve possible triplet combinations (ABA; ADA; BAB; BDB; DAD; DBD; DBA; BDA; DAB; ADB; BAD; ABD) were equally frequent (± 1 triplet for two of the triplet conditions in each block). Triplets where the last trial had the same cue as the n-2 trial were categorized as back-switching triplets while triplets without that n-2 cue repetition were categorized as baseline triplets.

All participants received both written and oral task instructions and were asked not to keep track of previous trials. To make sure that the participants understood the instructions and kept the rules in mind,