Reward valence modulates conflict-driven attentional adaptation: Electrophysiological evidence

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ABSTRACT

Recent findings suggest that, relative to negative feedback, positive feedback counteracts conflict processing and subsequent attentional adaptation. Here we hypothesize that this interaction may direct adjustments in perception and action via the anterior cingulate cortex (ACC). We recorded EEG while participants performed an arrow flanker task with monetary gain or loss as arbitrary reward feedback between trials. As predicted, we found a reduction in conflict-driven adaptation for trials in which conflict was followed by monetary gain (vs. monetary loss), a behavioral effect accompanied by a modulation in early visual processing related to the processing of the distracters. Moreover, time-frequency analyses showed that ongoing fronto-central theta oscillations induced by previous conflict sustained longer after loss than after gain, an interaction presumably reflecting ACC modulation. These data provide a first important step toward understanding the neural mechanism underlying the affective regulation of conflict-driven behavior.

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1. Introduction

When people face adverse events, they typically adapt their attentional resources to deal with this demand. This adaptation of cognitive effort and attentional control has been reported for numerous changes in situational demands varying from increases in task difficulty (Botvinick et al., 2001; Dreisbach and Fischer, 2011; Gratton et al., 1992; Hillgruber, 1912), the experience of stressful and aversive stimulation (Easterbrook, 1959; Finkelmeyer et al., 2010; Hommel et al., in press) to the registration of performance errors (Ridderinkhof et al., 2004). More recent work shows that positive affective states may undo or neutralize the impact of these adverse events whereas negative affective states may potentiate their impact (Cabanac, 1971; Fredrickson et al., 2000; Leknes and Tracey, 2008; van Steenbergen et al., 2009, 2010, in press). Thus, aversive and rewarding events may compensate for each other's effects, possibly via a common mechanism that aims at behavioral optimization (Cabanac, 1992; Botvinick, 2007).

The anterior cingulate cortex (ACC) is thought to play an important role in this optimization process (Botvinick et al., 2001; Gehring and Willoughby, 2002; Holroyd et al., 2008). Event-related brain potential (ERP) studies have shown that the ACC generates a mediofrontal negativity wave, called the N2 component, which can be elicited by conflict, as triggered by competing responses in tasks where participants need to focus on a relevant target while ignoring distracting information (Forster et al., 2011; Yeung et al., 2004). It has been suggested that feedback stimuli signaling positive events and reward may inhibit this neural conflict signal, as evidenced by an opposite, positive-going, deflection in the ERP with a similar temporal and spatial distribution as the N2 component (Holroyd et al., 2008; Holroyd and Coles, 2002). These and other data suggest that reward valence may interact with conflict monitoring activity in the ACC, presumably via phasic dopamine signaling from the midbrain (Jocham and Ullsperger, 2009; Munte et al., 2008; Schultz, 2007).

The present study was designed to investigate whether these reward valence effects on neural conflict monitoring may account for the recent observation that unexpected monetary gain, relative to loss, prevents the adaptive upregulation of attentional control in conflict-inducing flanker tasks (van Steenbergen et al., 2009). In flanker tasks, participants respond to centrally presented visual targets while ignoring surrounding non-targets that may

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signal the same or a different response as the target (Eriksen and Eriksen, 1974). The degree to which performance is worse in response-incompatible as compared to response-compatible trials can be taken to reflect the participant's ability to focus on relevant information in the face of distraction. Interestingly, the size of this compatibility effect is typically reduced in trials following incompatible trials (the so-called conflict-adaptation effect; Gratton et al., 1992), which has been taken to reflect a conflict-induced sharpening of the attentional focus (e.g., Botvinick et al., 2001; Egner, 2007). However, we have recently shown that unexpected positive feedback, in comparison to negative feedback, presented immediately after a response in an incompatible trial (cf. Fig. 4A) eliminates the conflict-adaptation effect, presumably by counteracting attentional adaptation to conflict (van Steenbergen et al., 2009). Given the well-known role of the ACC in producing adaptive behavior, this effect of reward valence on subsequent adaptation might be driven by a modulation of ongoing oscillatory neural activity produced by previous response conflict (Botvinick et al., 2001; Cohen et al., 2008; Kerns et al., 2004).

Traditional ERP techniques are not suitable to address this hypothesis because averaging single-trial EEG traces will reveal only neural activity that is phase-locked to the onset of the stimulus (cf. Luu et al., 2004; Yeung et al., 2004). In contrast, time-frequency decomposition analyses such as complex wavelet convolutions can assess sustained conflict-related processing in flanker, Stroop, and Simon tasks (Cavanagh et al., 2009; Cohen et al., 2008; Hanslmayr et al., 2008). Wavelet analyses are sensitive to oscillatory activity that varies in phase from trial to trial and can provide measures of instantaneous power (i.e., energy at different frequencies, a.k.a. induced activity) and inter-trial phase coherence (i.e., consistency of oscillation onset across trials, a.k.a. evoked activity). Cumulating evidence suggests that ongoing fronto-central midline theta (4–8 Hz) power measured at the scalp can be modulated by conflict (Cohen et al., 2008; Hanslmayr et al., 2008) and feedback processing (Cohen et al., 2007, 2009). As implied by intracranial recordings, this theta effect may originate from the ACC and the surrounding medial frontal wall (Cohen et al., 2008). Based on these observations, we hypothesized that oscillations in the theta band may reflect the actual conflict parameter and the effects of reward valence on the conflict state, and thus show a conflict-induced increase that, relative to negative feedback, is attenuated by subsequent unexpected positive feedback.

A second aim of the present study was to test the idea that conflict and reward valence do not only co-modulate subsequent selective attention and the resulting behavioral adaptation (cf. van Steenbergen et al., 2009), but also alter early distracter processing in the visual cortex. Thus, if conflict on a previous trial intensifies the attentional focus on the target on the subsequent trial, this should be accompanied by a shallower processing of the surrounding flankers (cf. Treue, 2001). Reward valence may counteract this effect. Evidence for distracter-related modulation in the visual cortex in humans has mainly been provided by fMRI studies on the effect of perceptual and working memory load on attentional focus (for a review, see Lavie, 2005). Reduced distracter activation in visual cortex has also been reported during post-error adaptation (Danielmeier et al., 2011). However, there is no evidence yet that conflict in correct responses triggers a similar adaptation (Egner and Hirsch, 2005). In order to test this possibility, our task used vertically moving flankers that elicit a motion-sensitive ERP component in the visual cortex known as the motion visual evoked potential (motion VEP; for a review, see Heinrich, 2007). Using the motion VEP as an index of distracter-related processing, we hypothesized it to be sensitive to the modulation of attentional focus triggered by the interaction between reward valence and conflict on the preceding trial.

To summarize, we predicted that (1) conflict induced by incompatible flankers increases fronto-central midline theta oscillations and sharpens the attentional focus, thus decreasing distracter-related visual processing and behavioral compatibility effects in the subsequent trial; and (2) the presentation of a positive (vs. negative) stimulus immediately after an incompatible trial counteracts these neural and behavioral effects. This was tested in a flanker task by providing unpredictable monetary gains or losses during the response-stimulus interval (see Fig. 4A). Neutral trials, without gain or loss, were also included to provide a baseline condition.

2. Methods

2.1. Participants

Thirty-three right-handed university students participated (18–27 years of age; 6 men and 27 women). They were informed about the duration of the experiment (2 h, including EEG preparation) and that they would earn €13 (or course credits), plus a bonus that could increase to a few euros if they were lucky. Three participants were excluded from analyses because of technical problems during the acquisition of the physiological data. The experiment was conducted in accordance with relevant regulations and institutional guidelines and was approved by the local ethics committee from the Faculty of Social and Behavioral Sciences. All students read and signed informed consent.

2.2. Experiment

Subjects were informed about the task and that positive, negative, and neutral cartoon faces (smilies, grumpies, and neutral faces) would appear between trials independent of their actual performance being fast/slow or correct/erroneous. The computer would add €0.20 to their bonus if a smiley appeared and would subtract €0.20 if a grumpy appeared. Neutral cartoon faces were not associated with any gain or loss. Subjects were encouraged to make quick and accurate responses with their index fingers, to the central target of an arrow stimulus array. After informed consent, EEG preparation and a 6-min resting state EEG measurement, participants performed 24 practice trials in which they were given accuracy feedback for 600 ms at the end of each trial. Following this practice block, subjects performed a motion localizer block with 168 randomly presented flanker trials half of which use moving and half of which use still flankers (not followed by any faces or feedback). These trials started with a fixation cross (800–1000 ms, jittered), after which the stimulus array was presented until a response was given (maximum duration of 1000 ms).

Task instructions were repeated before the test trials started. Participants were informed about the seven blocks in which they would earn money, each lasting about 5 min. Self-paced break screens were shown in between. We did not tell the subjects that the last test block annexed a filler block of 36 trials, where gain trials were over-represented. This resulted in a random bonus payoff of between €1.60 and €4.00 for each person. The stimuli were presented on a white background on a 17-in. CRT monitor (1024 × 768 pix), and participants viewed the monitor from a distance of about 60 cm. Each of the 840 test trials started with a fixation cross (900–1100 ms, jittered), followed by the stimulus array (99 × 7 pix) that always comprised a target without motion and four vertically moving flankers. Unlike in the motion localizer trials, flankers in the test block were always moving. The amplitude of the vertical movement flankers made was 10 pixels (about 0.3°). The vertical movement deviated around the vertical center of the screen, and can be described by a triangular wave (that is, flankers moved with a constant speed up and down) with a period of 200 ms. Targets and flankers were black arrows pointing either left or right. We used the same number of compatible (flankers in the same direction as the target) and incompatible (flankers opposite to the target) trials. Almost immediately (30 ms) after a response to the stimulus array or, in the case of omission, after 1000 ms, a yellow line-drawn face (200 × 200 pix) was presented for 750 ms, after which the next trial started. The three types of cartoon faces appeared with equal probability and served to indicate monetary gain or loss.

2.3. EEG recording

Electroencephalographic (EEG) activity was recorded over thirty positions: AFz, F5, Fz, F6, FC3, FCz, FC4, C5, C3, C1, Cz, C2, C4, C6, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, POz, PO8, O1, Oz, and O2 of the 10/10 standard. Horizontal eye movements were calculated by bipolar derivations of electro-oculogram (EOG) signals over the left and right outer canthus. Vertical eye movements were calculated by bipolar derivations of signals above and below the left eye. Monopolar recordings were referenced to the common mode sensor (CMS) and drift was corrected with a driven right leg (DRL) electrode (for details see http://www.biosemi.com/faq/cms&drl.htm). In order to re-reference the data off-line, two electrodes were placed at the left and right mastoid. Signals were DC amplified and digitized with a BioSemi ActiveTwo system at a sampling rate of 512 Hz.