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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.

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 offline, 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.

2.4. Data analysis

2.4.1. Behavioral data

Repeated measures analysis of variance (ANOVA) and *t*-tests were used to analyze correct reaction time (RT) and error rates for test trials at Trial N + 1, as a function of the compatibility of Trial N + 1 (I vs. C); the compatibility of Trial N (incompatible/conflict vs. compatible/no conflict); and the reward signal (gain, neutral, or loss), shown as arbitrary feedback after Trial N, see Fig. 4A. We also calculated simple effect scores for each reward condition separately. Compatibility effects were calculated for reaction times or error rates according to the following formula: (cI + iI)/2 – (cC + iC)/2. Conflict-adaptation effects were calculated as follows: (cI – cC) – (iI – iC). To provide a stable baseline for conflict and reward at the trial N, we only included those trial sequences that followed correct responses and neutral feedback. In addition, the first two trials of each block, trials following an error, and trials with RTs not fitting the outlier criterion (2 SDs from the individual condition-specific mean) were excluded from the analysis.

2.4.2. EEG analyses

Off-line analyses were performed with Brain Vision Analyzer. After rereferencing the channels to the average mastoid, data were high-pass filtered 0.01 Hz (24 dB/oct), and ocular artifacts were corrected using the standard Gratton et al. (1983) method. EEG artifacts were automatically identified using four criteria: (1) bad gradient (>50 μV/sample), (2) bad max–min difference (>200 μV/200 ms), (3) bad amplitude (absolute value > 1000 μV), and (4) low activity (<0.50 μV/100 ms). Before this procedure was applied, artifacts caused by high scalp impedance of a particular electrode were corrected on an individual basis (2 participants), using a linear derivation of surrounding electrodes. Artifacts elicited by power line noise were also corrected on an individual basis (15 participants) using a low-pass 50 Hz filter (24 dB/oct). Stimulus-locked artifact-free segments were created for EEG activity during the motion localizer block and during the test trials. For the test trials we used exactly the same trials as those used for behavioral RT analyses, provided they were artifact free (see above). This resulted in 33 trials per condition on average, for each subject.

Fronto-central theta oscillations (at electrodes Fz, FCz, and Cz) as a function of compatibility and reward at Trial N segments were analyzed using a Continuous Wavelet Transformation as implemented in Brain Vision Analyzer (Morlet Complex waveform, frequency range from 2.5 to 50 Hz in 30 logarithmic steps, Morlet parameter $c = 4.5$). Induced power was calculated by averaging across trials after a percent change baseline correction from −300 to −100 ms. Because power measures also comprise phase-locked activity, the amount of phase coherence was calculated separately. Phase coherence was estimated using the Phase Locking Factor solution (version 1.1; 103), and was baselined from -300 to -100 ms for statistical analyses. After visual inspection, statistical analyses were conducted by entering average theta band (4–8 Hz) power and phase coherence values from 200 to 500, 500 to 800, and 600 to 700 ms windows for each condition into repeated measures ANOVAs and paired *t*-tests. For these analyses, we focused on data from electrode Cz because it showed the maximum modulation of reward on conflict-induced theta oscillation.[1]

Motion VEPs were identified in the motion localizer block by comparing ERPs elicited by moving flankers and still flankers. The Motion VEP was measured as the average ERP values from a window of 160 to 220 ms in occipital and occipito-temporal electrodes, using a 200-ms pre-stimulus baseline (cf. Heinrich, 2007). Statistical analyses (repeated-measures ANOVAs) of motion-related ERPs in the test trials at Trial N + 1 segments were focused on electrode sites that showed a motion VEP maximum in the localizer block. Greenhouse–Geisser correction was applied whenever appropriate. For illustrative purposes, a 50-Hz low-pass filter was applied to all grand averages shown in Fig. 3.

3. Results

3.1. Behavioral data

As shown in Fig. 1 and Table 1 (see also summary in Fig. 4C), the flanker task produced standard RT compatibility effects across feedback conditions, indicating faster performance on compatible than on incompatible trials. Standard conflict adaptation should yield an interaction between current- and previous-trial compatibility, such that the interference effect is smaller after conflict (incompatible) trials than after non-conflict (compatible) trials, presumably reflecting enhanced control and attentional focus (cf. Egner, 2007). This reduction in interference in the flanker task usually is driven by both post-conflict speeding of incompatible trials (illustrating that increased focus reduces interference) and post-conflict slowing of compatible trials (illustrating that increased focus reduces facilitation). A trend for this standard conflict-adaptation effect was found in the loss condition, $t(29) = 1.88$, $p_{1\text{-sided}} < .05$, although not in the neutral condition, $t(29) = 0.12$, $p = .90$). A reversed conflict-adaptation effect was observed for the gain condition, $t(29) = 2.04$, $p = .05$. Replicating our earlier observation (van Steenbergen et al., 2009), a direct comparison of the gain and the loss conditions confirmed the predicted effect of reduced conflict adaptation in the gain vs. the loss condition for RT, as shown by a significant compatibility$_N$ (2) × reward (2) × compatibility$_{N+1}$ (2) interaction, $F(1,29) = 6.04$, $p = .02$, MSE = 333.73, $\eta_p^2 = .172$ (see Table 1 for details). The reward (2) × compatibility$_{N+1}$ (2) interaction was also significant, $F(1,29) = 5.46$, $p = .03$, MSE = 345.21, $\eta_p^2 = .158$.

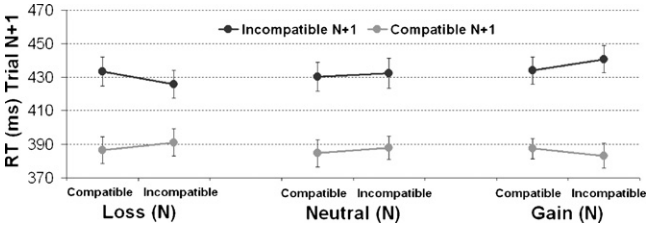

Fig. 1. Sequential adaptation in correct reaction times (RT) at Trial N + 1, as a function of compatibility and reward at Trial N, and current compatibility at Trial N + 1. The loss condition yielded standard conflict adaptation, that is a reduction of the compatibility effect (=RT incompatible N + 1 – RT compatible N + 1) after an incompatible (vs. compatible) trial at trial N. This effect is absent in the neutral condition and reversed in the gain condition.

An ANOVA including all three levels of reward suggested a trend for a 3-way interaction effect, $F(1,58) = 2.54$, $p = .087$, MSE = 396.48, $\eta_p^2 = .081$. Subordinate ANOVAs showed that the effect of reward on conflict-adaptation modulated the compatibility effect adjustment following conflict (incompatible) trials, $F(2,58) = 6.60$, $p = .003$, MSE = 594.49, $\eta_p^2 = .185$, but did not affect the compatibility effect adjustments after no-conflict (compatible) trials, $F(2,59) = 0.02$, $p = .98$, MSE = 843.52, $\eta_p^2 = .001$. A planned *t*-test focusing on trials following incompatible trials (see also summary in Fig. 4C, black bars) indicated an increased compatibility effect for gain in comparison to the neutral, $t(29) = 2.09$,

Table 1
Behavioral data for each condition.

	RT (ms)	Error rate (%)
Loss condition		
Compatible trial following a compatible trial (cC)	387	1.0
Compatible trial following an incompatible trial (iC)	391	0.4
Incompatible trial following a compatible trial (cI)	433	6.4
Incompatible trial following an incompatible trial (iI)	426	2.5
Compatibility effect	41	3.8
Conflict-adaptation effect	12	3.3
Neutral condition		
Compatible trial following a compatible trial (cC)	385	1.6
Compatible trial following an incompatible trial (iC)	388	0.4
Incompatible trial following a compatible trial (cI)	430	6.7
Incompatible trial following an incompatible trial (iI)	432	4.2
Compatibility effect	45	4.4
Conflict-adaptation effect	1	1.2
Gain condition		
Compatible trial following a compatible trial (cC)	388	1.0
Compatible trial following an incompatible trial (iC)	383	0.0
Incompatible trial following a compatible trial (cI)	434	6.8
Incompatible trial following an incompatible trial (iI)	441	2.6
Compatibility effect	52	4.1
Conflict-adaptation effect	−11	3.2

Note: The compatibility effect was calculated for reaction times or error rates according to the following formula: (cI + iI)/2 – (cC + iC)/2. The conflict-adaptation effect was calculated as follows: (cI – cC) – (iI – iC).

[1] We also have performed wavelet analyses on feedback-locked segments. This analysis yielded a pattern of results similar to the stimulus-locked analysis reported in this article.

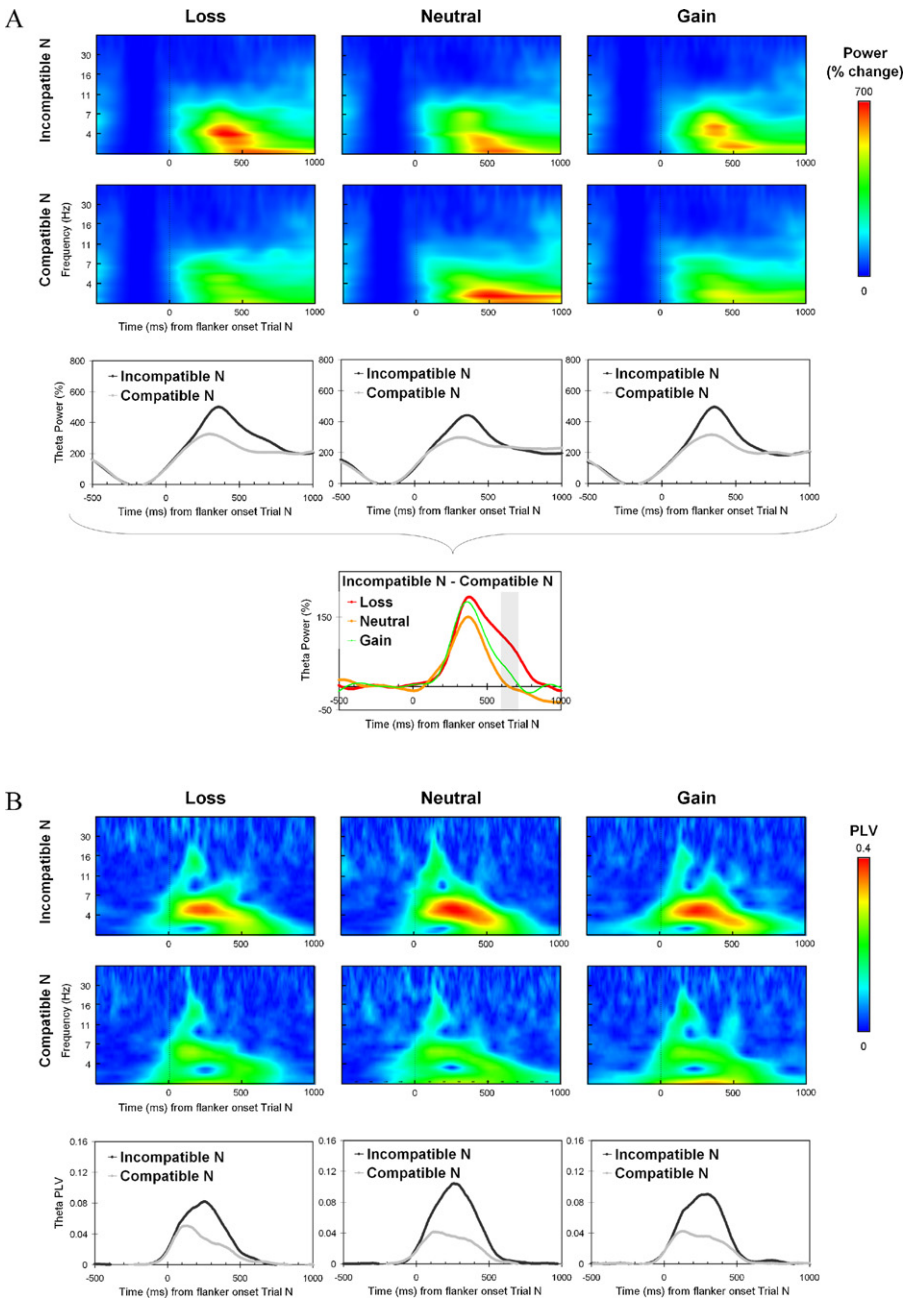

Fig. 2. Effect of conflict and reward at Trial N on frequency power (A) and phase coherence as indicated by phase locking value (B) at electrode Cz. In comparison to gain feedback, induced theta (4–8 Hz) power sustained longer for incompatible vs. compatible flankers after loss feedback.

$p = .045$, and the loss condition, $t(29) = 3.81$, $p = .001$, but no differences between the neutral and loss condition, $t(29) = 1.46$, $p = .154$. Error rate data showed significant main effects for compatibily$_{N+1}$ (indicating more errors for incompatible trials) and compatibily$_{N}$ (indicating fewer errors after incompatible trials), but no (higher-order) interactions (see Table 1 for details). Thus, the modulation of conflict-adaptation in RT was not accompanied by a speed-accuracy trade off.

3.2. Theta frequency dynamics

One subject was excluded from these analyses because of an insufficient number of trials (20 trials per condition on average) to perform reliable wavelet analysis, leaving 29 subjects available for this analysis. Fig. 2 shows the power and phase coherence measures of theta oscillations as induced by flanker compatibility at trial N and subsequently modulated by the feedback immediately following a key press to the stimulus array. Based on visual inspection, we analyzed two subsequent 300-ms intervals starting at 200 ms after stimulus onset. During the first time window (200–500 ms), an initial theta response to the stimulus array was observed to be greater for incompatible than compatible trials This response appeared to be at least partly phase-locked to the stimulus, because this effect was not only observed in the power measure, $F(1,28) = 15.66$, $p < .001$, MSE = 46952.06, $\eta_p^2 = .359$, but also in the phase locking value measure, $F(1,28) = 4.67$, $p = .039$, MSE = .029, $\eta_p^2 = .143$. More importantly, as predicted, induced theta power sustained longer for incompatible vs. compatible flankers during a subsequent 500–800 ms interval after loss feedback, $t(18) = 3.02$, $p = .005$ but not after gain feedback, $t(18) = 1.15$, $p = .59$, or neutral feedback,

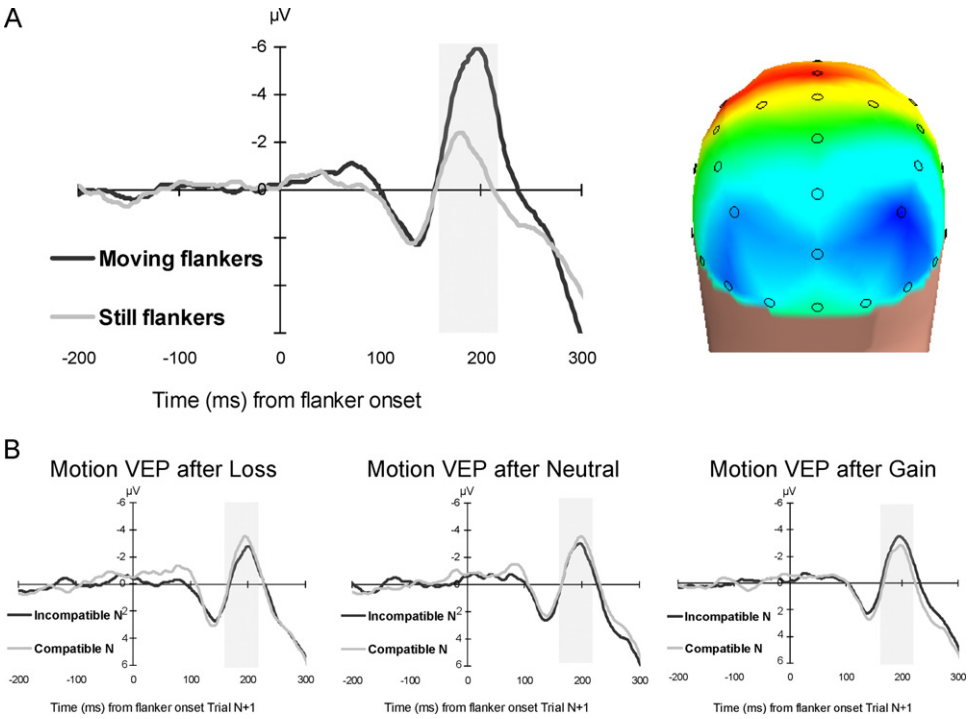

Fig. 3. (A) In the motion localizer block, moving flankers in comparison to still flankers elicited a standard motion VEP with an occipito-temporal scalp distribution. (B) During test trials, conflict and reward at Trial N modulated the motion VEP elicited at Trial N + 1. Consistent with behavioral interference effects, conflict on the previous trial reduces flanker-related motion processing in the subsequent trial for the loss condition. The reversed pattern is shown for the gain condition. All data are taken from electrode P4.

$t(18) = .37$, $p = .71$. As shown in Fig. 2 (see also summary in Fig. 4B), this modulation of reward on ongoing theta activity was maximal at the 600–700 ms interval, yielding a compatibility$_N$ (2) × reward (3) interaction effect, $F(2,56) = 3.26$, $p = .046$, MSE = 10013.82, $\eta_p^2 = .104$. Following incompatible trials, loss yielded more theta power in comparison to gain, $t(28) = 2.30$, $p = .029$, or neutral feedback, $t(28) = 2.10$, $p = .045$, whereas there was no difference between gain and neutral feedback, $t(28) = 0.32$, $p = .75$.

No interaction was observed in phase locking value ($F < .5$), indicating that the effects observed in power cannot be attributed to effects driven by phase-locked theta activity.

3.3. Distracter-related visual processing

The motion localizer task did not elicit a significant motion VEP (ERP of moving flankers minus ERP of still flankers) in each single participant. In order to still identify the motion-relevant electrodes, we included only those participants who actually showed a motion VEP amplitude > 2 μV in both hemispheres during the motion localizer block (cf. Heinrich et al., 2006). Fig. 3A shows the data of the remaining 14 participants. In comparison to still flankers, moving flankers elicited a standard motion VEP dominated by an occipito-temporal negativity that peaked around 200 ms and reached its maximum value ($ps < .001$) in both hemispheres at electrode-pair P3/4.

Analyses on the motion-related activity during the test trials were run both for this subset of participants (showing the strong motion-sensitive activity in the localizer) and for all participants as a group. Because both analyses showed the same pattern, the analysis on all participants is reported only. Direct comparison of the loss and gain conditions revealed a compatibility$_N$ (2) × reward (2) interaction in the motion VEP elicited by Trial N + 1 for electrode P4 ($F(1,29) = 11.68$, $p = .002$, MSE = 1.09, $\eta_p^2 = .287$), but not for electrode P3 ($F(1,29) = 2.58$, $p = .11$, MSE = 0.96, $\eta_p^2 = .085$). Fig. 3B (see also summary plot in Fig. 4D) illustrates this interaction. A planned t-test indicated increased (more negative VEP) distracter-related motion activation following incompatible trials after gain in comparison to loss ($t(29) = 3.14$, $p = .004$). Thus, this pattern mirrors the interference-effect modulation observed in behavior: conditions characterized by more behavioral interference from the flankers are accompanied by more motion VEP activity related to the processing of these flankers (compare Fig. 4C and D). When the ANOVA included the neutral condition, the same interaction emerged, $F(2,58) = 3.95$, $p = .034$, MSE = 2.26, $\eta_p^2 = .120$. Analyses showed that there were no differences when comparing incompatible trials after the neutral condition with the gain condition ($t(29) = 1.33$, $p = .19$) or the loss condition ($t(29) = 1.15$, $p = .26$). We also analyzed whether behavioral conflict-adaptation effects were positively correlated with conflict-driven reductions (less negative activity) in motion VEP activity across all subjects. Indeed, this correlation was observed for the gain condition ($r = 0.397$, $p = .029$), indicating that the more gain led to a reversal of the conflict-adaptation effect, the more increased distracter-related activity was observed after conflict relative to no-conflict. This correlation was not observed for the neutral, or loss conditions ($ps > .25$).

4. Discussion

The goal of the present study was to investigate the impact of interactions between conflict and reward valence processing on behavioral and neural adaptation. The behavioral effects replicated our earlier study (van Steenbergen et al., 2009) in showing reduced conflict-driven attentional adaptation in the gain condition when compared to the loss condition. However, while in the previous study conflict adaptation was present in the neutral condition, this was not the case in the current study. This general reduction of adaptation might have been due to the fact that our study took about 2 h to finish. As compared to the 15 min of our earlier study, this was likely to influence motivation and deplete

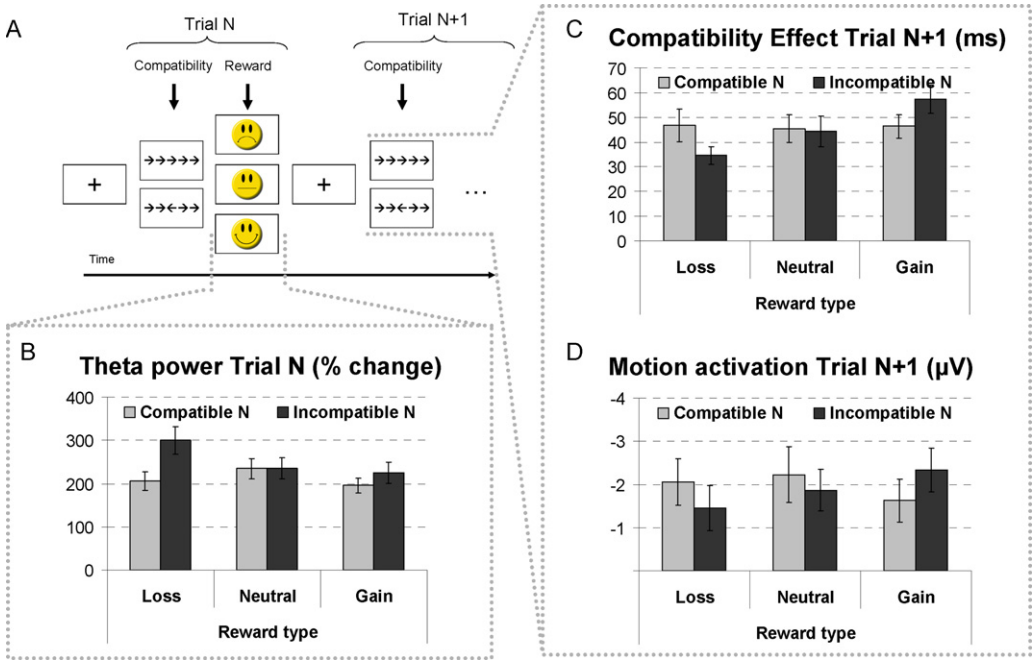

Fig. 4. (A) Illustration of the experimental design. It was hypothesized that conflict induced by incompatible trials at Trial N is counteracted by subsequent gain (vs. loss) feedback; this would reduce conflict-driven attentional focusing at Trial N + 1. (B–D) Summary of the main findings: In comparison to the loss condition, gain reduced conflict-induced fronto-central theta power measured at Cz in the 600–700 ms interval at Trial N (B), and reduced conflict-driven focusing at Trial N + 1 as measured in behavioral compatibility effects (=RT incompatible N + 1 − RT compatible N + 1) (C), also mirrored in distracter-related visual processing as indexed by the motion VEP measured at P4 in the 160–220 ms interval (D).

attentional resources—conditions that are known to work against conflict adaptation (Fischer et al., 2008).

Our study yielded two novel findings (see summary in Fig. 4). First, as predicted, fronto-central theta power appears to reflect the compensatory effects of reward valence on conflict-related neural activity, as was shown by a sustained theta response during monetary loss, which was absent in the gain condition. This theta oscillation response may originate from the ACC and may represent a signal that indicates the need for more cognitive control, thus driving the sharpening of the attentional focus observed on the subsequent trial (Cohen et al., 2008). Such modulation may involve dopamine signaling from the midbrain. It has been hypothesized that such fronto-striatial interactions may lower prefrontal dopamine concentrations, which shifts the balance of receptor activation toward D1 receptors, thus reducing distraction and improving attentional focusing (Jocham and Ullsperger, 2009; cf. Frank, 2005; Holroyd et al., 2008; Holroyd and Coles, 2002). Our data suggest that theta oscillations may play an important role in this modulation. Further research is needed to understand the functional role of theta oscillations in the presumed interactions with dopamine neurons and other brain areas involved in the regulation of cognitive control.

The second novel finding concerns the modulation of distracter-related motion activation in the visual cortex as assessed by means of the motion VEP in the right hemisphere. Because the flankers always moved during the test trials, we could use the motion VEP to measure the extent to which the flanking distracters were visually processed and modulated by previous conflict and feedback. We predicted that reduced behavioral interference by the flankers (driven by improved attentional focus) may be accompanied by reduced neural processing of the flankers (as measured by the motion VEP). In order to identify the relevant motion-related electrodes, we analyzed ERPs in a separate motion-localizer block for those participants who showed a strong neural response to motion. Subsequent analyses of the test trials for both this subset of participants and all participants as a group showed that behavioral adaptation in the subsequent trial was accompanied by a corresponding adjustment in distracter activation in the visual cortex (compare Fig. 4C and D). Thus, as predicted, increased behavioral interference by the flankers was associated with increased motion-related activation (elicited by these flankers). Note that an earlier study by Egner and Hirsch (2005) using fMRI did not find a distracter-related attenuation after conflict in a Stroop task. Our study points to the interesting possibility that ERP studies may actually be more sensitive to this modulation than BOLD responses are. Alternatively, it is possible that Stroop performance relies on different strategies than flanker task performance (cf. Lavie, 2005).

Two limitations of the present study need to be mentioned. First, as in the previous report, the reward manipulation affected behavioral and neural adaptation rather mildly, even though our sample was relatively large ($N = 30$). Second, when the neutral condition was included in the comparisons, statistical power to detect reward-related differences dropped, especially for the motion VEP analyses. One possible explanation of the larger inter-individual differences in the neutral condition might be that participants showed more variation in their appraisal of the situation of neither losing, nor winning any money. In other words, participants may have experienced the neutral condition as either a positive or negative situation, depending on subjective expectancies and affective state context (cf. e.g. Larsen and Norris, 2009). As a consequence, the effects observed in behavioral and neural adaptation were most robust when the most extreme values in reward valence were contrasted, that is when the gain and loss conditions were compared directly (as in van Steenbergen et al., 2009). Conflict followed by neutral feedback in behavioral and neural adaptation showed intermediate values, in between the loss and the gain condition (compare black bars in Fig. 4), but statistically not significantly different from (1) the loss condition for behavior, (2) the gain condition for theta oscillations, and (3) both conditions for the motion VEP analyses. The most parsimonious interpretation of this pattern of results is that reward valence interacts with conflict processing. Thus, it is likely that the effects observed are driven by a

combination of gain-inhibiting (cf. Holroyd et al., 2008) and loss-potentiating effects, and our findings cannot be used as evidence for or against only one of these alternatives.

In line with our valence interpretation, other studies using tonic affect manipulations also have shown that, irrespective of arousal changes, positive mood decreases and negative mood increases conflict adaptation (Kuhbandner and Zehetleitner, 2011; van Steenbergen et al., 2010, in press). Given that feedback in our study was presented independently of the actual response made by the participants, and given that participants were informed about this in advance, feedback was unexpected and unconfounded with performance on the previous trial. This aspect of the task may have been crucial for the effect of positive emotions leading to a canceling out of the presumably aversive state associated with conflict (cf. Fredrickson et al., 2000), rather than acting as an (implicit) motivator (Custers and Aarts, 2005) to enhance subsequent performance. Indeed, as recently shown by Sturmer et al. (2011), when feedback is contingent on performance in a Simon task, reward can actually increase conflict adaptation, probably because this task characteristic led participants to appraise this feedback as an incentive signal. This recent finding thus points to an important potential difference between the incentive/motivational and the affective impact reward feedback can have on task performance, and future studies need to dissociate these effects (cf. Gable and Harmon-Jones, 2011; for a review of differential effects of affect and motivation, see Chiew and Braver, 2011). Conversely, with respect to negative affect, a recent study has shown that not all negative emotions will necessarily increase conflict adaptation either. Using high-arousal negative pictures, such as mutilated bodies, presented as arbitrary stimuli in between Stroop trials, Padmala et al. (2011) found evidence for reduced rather than increased conflict adaptation (in comparison to neutral pictures). Negative emotions thus cannot only facilitate conflict detection; when high in arousal level they may also expend or divert resources needed for control implementation (cf. Pessoa, 2009). However, future studies have to demonstrate whether these effects are specific for high-arousal negative emotions, or whether similar effects can be observed when positive high-arousal stimuli (e.g., erotic pictures) are used.

To conclude, this study demonstrates that conflict triggered by incompatible trials in a flanker task increases fronto-central midline theta oscillations and sharpens the attentional focus, thus decreasing distracter-related visual processing and behavioral interference in the subsequent trial. We showed that adaptation effects in behavior and visual cortex are counteracted by reward valence, which also involved the modulation of ongoing theta oscillations. These data provide a first important step toward understanding the neural mechanism underlying the affective regulation of conflict-driven behavior. Future studies are needed to understand how other factors such as motivation and arousal may also involve and modulate this neural system.

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