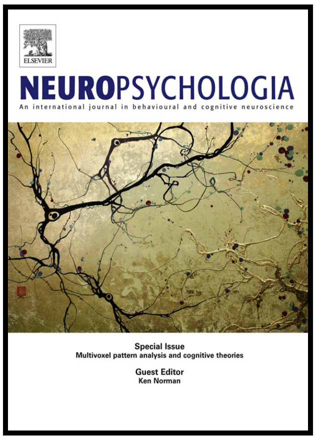
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Cognitive control modulates preferential sensory processing of affective stimuli

Marco Steinhauser[1,2*], Tobias Flaisch[2*], Marcus Meinzer[3], Harald T. Schupp[2]

[1]Department of Psychology, Catholic University of Eichstätt-Ingolstadt, Eichstätt, Germany

[2]Department of Psychology, University of Konstanz, Konstanz, Germany

[3]Centre for Clinical Research, University of Queensland, Brisbane, Australia

Marco.Steinhauser@ku.de
Tobias.Flaisch@uni-konstanz.de
[*]Correspondence should be addressed to: Marco Steinhauser. Catholic University of Eichstätt-Ingolstadt. Department of Psychology. Ostenstraße 25. D-85072 Eichstätt. Germany. Phone: +int (0)8421-93-21120
[*]Correspondence should be addressed to: Tobias Flaisch. University of Konstanz. Department of Psychology. Fach 36. D-78457 Konstanz. Germany. Phone: +int (0)7531-88-5129

Abstract

Adaptive human behavior crucially relies on the ability of the brain to allocate resources automatically to emotionally significant stimuli. This ability has consistently been demonstrated by studies showing preferential processing of affective stimuli in sensory cortical areas. It is still unclear, however, whether this putatively automatic mechanism can be modulated by cognitive control processes. Here, we use functional magnetic resonance imaging (fMRI) to investigate whether preferential processing of an affective face distractor is suppressed when an affective distractor has previously elicited a response conflict in a word-face Stroop task. We analyzed this for three consecutive stages in the ventral stream of visual processing for which preferential processing of affective stimuli has previously been demonstrated: the striate area (BA 17), category-unspecific extrastriate areas (BA 18/19), and the fusiform face area (FFA). We found that response conflict led to a selective suppression of affective face processing in category-unspecific extrastriate areas and the FFA, and this effect was accompanied by changes in functional connectivity between these areas and the rostral anterior cingulate cortex. In contrast, preferential processing of affective face distractors was unaffected in the striate area. Our results indicate that cognitive control processes adaptively suppress preferential processing of affective stimuli under conditions where affective processing is detrimental because it elicits response conflict.

Keywords:
emotion, cognitive control, face processing, functional magnetic resonance imaging, visual cortex

1. Introduction Detecting and responding to significant sensory events is crucial for an organism’s survival. Therefore, the human brain possesses potent mechanisms to direct attention automatically to affective stimuli like food or facial expressions (Lang, Bradley, & Cuthbert, 1997). This has been demonstrated by studies showing preferential processing of affective stimuli in sensory areas of the human brain (for overviews, see Vuilleumier, 2005; Vuilleumier, Armony, & Dolan, 2003). Although such a mechanism is usually beneficial because it allows an organism to efficiently prepare adequate behavioral responses, it can be detrimental under conditions where behaviors are triggered that interfere with current goals and intentions (McClure, Botvinick, Yeung, Greene, & Cohen, 2007; Ochsner & Gross, 2005). In the present study, we investigated whether cognitive control processes counteract such emotion-mediated conflicts by suppressing emotion processing in visual-associative areas. Our study aims to contribute to our understanding of affective processing in the visual system as well as the resolution of emotion-mediated conflicts.

A viable framework to examine the mechanisms underlying cognitive control and conflict resolution is the conflict monitoring theory (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter et al., 1998). It assumes that a conflict monitoring system registers response conflict emerging when contradictory behavioral tendencies become activated simultaneously, and then strengthens cognitive control to prevent the occurrence of further conflict. Behavioral evidence for this account has been provided by studies demonstrating so-called *conflict adaptation effects* (Gratton, Coles, & Donchin, 1992). In these studies, participants had to classify a target stimulus while ignoring distractor stimuli associated with the same (congruent stimulus) or a different response (incongruent stimulus) as the target. Crucially, incongruent stimuli were assumed to induce higher response conflict than congruent stimuli, which implies larger response times (RTs) and error rates for incongruent stimuli than for congruent stimuli. As predicted by conflict monitoring theory, the effect of response conflict on the current trial was determined by the amount of response conflict on the previous trial. More specifically, the effect of response conflict was smaller following a trial with high response conflict than following a trial with low response conflict (Gratton et al., 1992; Ullsperger, Bylsma, & Botvinick, 2005).

In recent years, the neural basis of this conflict adaptation effect was investigated in a number of studies. Cumulative evidence suggested that the medial frontal cortex registers the occurrence of response conflict (e.g., Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Ullsperger & von Cramon, 2001) and causes the dorsolateral prefrontal cortex (DLPFC) to increase selective attention on the subsequent trial (e.g., Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000). This, in turn, leads to stronger activation of task-relevant information (Egner & Hirsch, 2005) and/or inhibition of task-irrelevant information (Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011; King, Korb, von Cramon, & Ullsperger, 2010).

However, recent studies demonstrated that if conflicts are mediated by emotional categories, different neural systems and different control processes are involved (Egner, Etkin, Gale, & Hirsch, 2008; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Etkin, Egner, &

Kalisch, 2011; Maier & di Pellegrino, 2012; Mohanty et al., 2007; Monti, Weintraub, & Egner, 2010; Saunders & Jentzsch, 2013; Soutschek & Schubert, 2013). When participants had to discriminate between fearful and happy faces while ignoring congruent or incongruent emotional words (“anxious”, “happy”), high response conflict led to decreased activity in the amygdala on the subsequent trial (Egner et al., 2008; Etkin et al., 2006). Moreover, the rostral anterior cingulate cortex (rACC) rather than the DLPFC was involved in the resolution of this emotion-mediated response conflict (Egner et al., 2008; Etkin et al., 2006). These results were interpreted as evidence that the resolution of emotion-mediated conflicts differs from that of other types of response conflicts. More specifically, the hypothesis was formulated that emotion-mediated conflicts are not resolved by enhancing selective attention but rather by suppressing emotional processing in the amygdala (Egner et al., 2008; Etkin et al., 2006).

The question emerges why mechanisms of conflict resolution differ depending on whether conflicts are mediated by affective or non-affective stimulus categories. One reason could be that increasing selective attention is not efficient in the case of an affective distractor because affective stimuli automatically attract attention. It is well-known that affective stimuli produce increased activity in sensory pathways (Vuilleumier, 2005; Vuilleumier et al., 2003), suggesting that these stimuli are preferentially processed already at very early stages of the perceptual system. For instance, affective (especially fearful) relative to non-affective faces are associated with increased activity in striate cortex (Vuilleumier, Armony, Driver, & Dolan, 2001) as well as in category-specific and category-unspecific areas of extrastriate cortex (Morris et al., 1998; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Vuilleumier et al., 2001). Comparable effects have been reported utilizing a variety of different visual stimulus materials including naturalistic scenes (Flaisch et al., 2015; Junghöfer, Schupp, Stark, & Vaitl, 2005; Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004), gestures

(Flaisch, Schupp, Renner, & Junghöfer, 2009), body posture (de Gelder, 2006), and words (Herbert et al., 2009).

By integrating these findings on preferential processing with the accounts of Etkin et al., (2006) and Egner et al. (2008) on control of emotion-mediated conflict, one could hypothesize that the prevention or resolution of emotion-mediated conflicts requires that cognitive control mechanisms directly modulate preferential processing of affective stimuli in sensory areas. The goal of the present study was to investigate whether such a modulation can indeed be found. Following the rationale of conflict monitoring theory (Botvinick et al., 2001), we hypothesized that preferential processing of affective distractors in sensory areas should be reduced or even abolished when affective distractors have previously elicited a response conflict. Such a finding would extend previous findings on the control of emotion-mediated conflict (Egner et al., 2008; Etkin et al., 2006) by showing that cognitive control prevents emotion-mediated conflicts by suppressing preferential sensory processing of affective distractors. Accordingly, our study aims to specify the mechanisms proposed by this earlier work.

To investigate this, we adopted an experimental task that has previously been used in studies on conflict monitoring (Egner et al., 2008; Etkin et al., 2006), and modified it to obtain a measure of preferential processing of affective stimuli. Participants discriminated between emotional words (“anxious”, “happy”) while ignoring simultaneously presented affective and non-affective faces. Affective faces were either congruent or incongruent to the target words, and thus, induced either low or high response conflict. The amount of preferential processing was determined by comparing activity on trials with affective face distractors with activity on trials with non-affective face distractors. In contrast to previous studies (Egner et al., 2008; Etkin et al., 2006), we used word stimuli as targets and face stimuli as distractors because this allowed us to use face-specific activity as a marker of distractor processing. To increase the power of detecting preferential processing, we selectively analyzed voxels that responded to faces in a localizer task in which participants passively viewed face pictures. We predicted that preferential processing of affective face distractors in these voxels should vary as a function of response conflict on the previous trial. If preferential processing of affective stimuli is subject to cognitive control, then differences in activity between stimuli with affective face distractors and those with non-affective face distractors should be reduced following trials with high response conflict.

We tested this hypothesis separately for several areas along the ventral stream of visual processing: Striate areas (BA17), category-unspecific extrastriate areas (BA18/19), and the face-specific fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997). These a-priori regions of interest were chosen because preferential processing of affective faces has previously been demonstrated in these areas (Morris et al., 1998; Pessoa et al., 2002; Vuilleumier et al., 2001). In this way, we aimed to determine the exact stage at which the suppression of affective processing becomes effective. In addition, we investigated whether effects on preferential processing are related to activity in control-related areas that have previously been shown to underlie the control of emotion-mediated conflict (Egner et al., 2008; Etkin et al., 2006). To this end, we analyzed functional connectivity between visual areas and the rACC using psychophysiological interaction (PPI) analysis.

2. Materials and Methods

2.1 Participants

Fourteen right-handed participants (6 females) between 19 and 32 years of age (mean 25.7) with normal or corrected-to-normal vision participated in the study. Participants were recruited at the University of Konstanz and received either course credits or €5 per hour. The study was approved by the ethics committee of the University of Konstanz, and written informed consent was obtained from all participants.

2.2 Task and procedure

Stimuli comprised 20 happy faces, 20 fearful faces, and 20 neutral faces from the KDEF picture library (Lundqvist & Litton, 1998). Within each category, half of the faces were male or female, respectively, and all faces were in grayscale. The stimulus set for the localizer task comprised the 60 face stimuli as well as 20 grayscale pictures of houses (Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005). The stimulus set for the main task was generated by combining each face stimulus with the German words *ANGST* (*engl*. fear) and *FREUDE* (*engl*. happiness), written with capital letters in gray Arial font. The resulting 120 stimuli consisted of three stimulus categories (see Figure 1): In *neutral stimuli*, the facial expression was not affective. In *congruent stimuli*, the facial expression was affective and corresponded to the word. In *incongruent stimuli*, the facial expression was affective but differed from the word. The stimuli were presented using MR-compatible goggles (VisuaStim XGA, Resonance Technology Inc.) at a resolution of 800 x 600 pixels (virtual viewing distance: approximately 120 cm; field of display subtended visual angles of 30° x 23°). Overall, the stimuli subtended a vertical visual angle of 15.5° and a horizontal visual angle of 18.2°, while the overlaid words subtended vertically 1.8° and horizontally 8.1° (*ANGST*) and 9.5° (*FREUDE*), respectively.

Figure 1: Exemplary stimuli of the three stimulus categories.

The *localizer task* required participants to passively view a stream of rapidly presented picture stimuli. Each picture was presented for 1000 ms, immediately followed by the next picture. The stream consisted of 400 pictures divided into 20 randomly ordered blocks. Each block contained the 20 pictures from one category in random order, and there was no gap between blocks. As a result, each picture from the four categories was presented five times.

The *main task* required participants to discriminate between the words ANGST and FREUDE while ignoring the irrelevant faces. Each trial started with the presentation of the stimulus for 1000 ms. Participants were instructed to respond as fast as possible by pressing response buttons with the left or right index finger, respectively. In half of the participants, *ANGST* required responding with the left hand, and *FREUDE* required responding with the right hand. In the other half, the mapping was reversed. The inter-stimulus interval (ISI) was exponentially distributed with a mean of 3500 ms and a range of 3000 ms to 5000 ms (Dale, 1999). Each of the 120 face-word compounds was presented three times in random order, resulting in a total of 360 trials.

2.3 Data acquisition and analysis

Scanning was conducted using a 1.5 Tesla Philips Intera MR-System equipped with Power Gradients. For functional imaging, a T2*-weighted Fast-Field-Echo, Echo-Planar-Imaging (FFE-EPI) sequence utilizing parallel scanning technique (SENSE; Pruessmann, Weiger, Scheidegger, & Boesiger, 1999) was acquired. In-plane resolution was 3 x 3 mm and slice thickness was 4.5 mm (24 axial slices; no gap; FOV = 192 mm; acquisition matrix: 64 x 64 voxels; TE = 40 ms; flip angle = 90°; TR = 2 sec). In addition, a high-resolution T1-weighted structural scan was obtained for each participant to facilitate spatial normalization. Preprocessing (including slice-time correction, realignment, spatial normalization and smoothing at FWHM = [8 8 9] mm) and statistical analyses of the functional images were conducted using SPM8 (Wellcome Department of Imaging Neuroscience, University College London, UK; see Friston, Holmes, Worsley, Poline, & Frith, 1995). No participant displayed head movement exceeding 1 mm on any axis and thus all were included in further analysis.

The localizer task was analyzed in a block design incorporating covariates for all categories, i.e., fearful faces, happy faces, neutral faces, and houses. Additionally, six movement parameters obtained during realignment and an overall intercept were also included in the model. A high-pass filter with a cutoff period of 128 s, as well as global scaling was applied to the data before estimating the model parameters.

The main task was analyzed in an event-related design which included nine covariates-of-interest classifying each trial both in terms of stimulus category on the current trial (congruent, incongruent, neutral) as well as of stimulus category on the previous trial (congruent, incongruent, neutral). To improve model fit, several covariates-of-no-interest were additionally included in the design matrix: The experimental covariates’ time and dispersion derivatives, six movement parameters obtained during realignment and an intercept. Again, a high-pass filter with a cutoff period of 128 s, as well as global scaling was applied to the data. BOLD-activity associated with each experimental condition was determined by contrasting each covariate-of-interest with the implicit baseline.

To test the experimental hypotheses, we analyzed activity in several a priori regions-of-interest (ROIs) which included separate ROIs for striate and extrastriate visual cortex, as well as the FFA. To maximize statistical power, we utilized individual masks for each participant which combined anatomical a-priori assumptions and individual activity during the localizer task. Specifically, search volumes for striate and extrastriate ROIs were based on the anatomical locations of Brodmann Areas 17 (striate) and 18/19 (extrastriate), respectively, using the Brodmann atlas as implemented in the MRIcron software (http://www.mccauslandcenter.sc.edu/mricro/mricron/; Rorden and Brett, 2000). The a priori search volume for the FFA was generated by placing spheres with a radius of r = 15 mm around maximum probabilistic voxel coordinates reliably indicating the position of the FFA (MNI [-40, -49, -22] and MNI [42, -49, -23] for left and right hemisphere, respectively; Tahmasebi et al., 2012). In a second step, voxels within the striate and extrastriate search volumes were included in the individual masks if they reached a statistical threshold of $p < .01$ (uncorrected) when contrasting faces against the implicit baseline. As several participants showed no activated voxels surpassing this threshold in the FFA search volume, a lower threshold of $p < .05$ (uncorrected) was used for all participants to obtain the individual masks for the FFA. In a final step, mean beta values within the individually selected ROIs during the main task were computed separately for each participant and condition and were subjected to repeated measurement ANOVAs. Importantly, individual voxel selection for ROI analysis was based exclusively on activity found in the localizer task and was thus independent from the analyzed main task. Significant effects were followed up by means of post-hoc comparisons utilizing Tukey‘s HSD.

To shed light on possible sources of top-down modulation exerting cognitive control over higher-order visual cortical regions during preferential emotion processing, we conducted an additional PPI analysis (Friston et al., 1997). Since our analyses indicated that the effect of cognitive control was comparable regarding extrastriate regions and the FFA, we combined the extrastriate and FFA ROIs of each participant and utilized the resulting maps as individual seed regions. From these seed regions, we extracted the deconvolved time courses of activity which were adjusted for the effects of interest in the model. The PPI variable was then created by calculating the product of these time courses with the psychological variable of interest. Specifically, for this we utilized the contrast of [(emotional > neutral)$_{\text{n-1 incongruent}}$ > (emotional > neutral)$_{\text{n-1 congruent}}$] as this should bring forward activation increases in cognitive control regions modulating preferential processing due to the incongruency of the previous trial. For each participant, we then calculated a general linear model incorporating the PPI interaction term, the seed region time course, the psychological effect of interest, as well as the movement parameters as covariates-of-no-interest. Finally, the individual estimates of the PPI interaction resulting from these models were then entered in a random-effects analysis to assess PPI effects at the group level. Results were considered meaningful, if they reached a threshold of $p < .01$, uncorrected at the voxel level and $p < .05$, FWE-corrected at the cluster level. As we were specifically interested in comparing our data to previous reports regarding the possible involvement of regions in the rACC (Etkin et al., 2006; Egner et al., 2008), we also conducted a small volume correction (SVC) around according coordinates reported in the literature (Etkin et al., 2006). To optimally capture the location of the activation cluster reported in this study, we combined the two reported voxels and calculated their midpoint coordinates (MNI [-10, 42, 1]). SVC was then calculated for a sphere with a radius of 25 mm around these voxel coordinates (see Fig. 4B). Resulting clusters are reported in terms of size, statistical significance and the location of their peak voxels spaced more than 10 mm apart.

Finally, we also conducted standard second-level SPM analyses for several contrasts, i.e., our main interaction of interest ([emotional > neutral] $_{\text{n-1 congruent}}$ > [emotional > neutral] $_{\text{n-1 incongruent}}$), as well as relevant contrasts reported in the literature (conflict resolution: [incongruent $_{\text{n-1 incongruent}}$ > incongruent $_{\text{n-1 congruent}}$]; conflict: [incongruent $_{\text{n-1 congruent}}$ > incongruent $_{\text{n-1 incongruent}}$]). However, these analyses did not produce statistically significant results.

3. Results

3.1 Conflict adaptation effects in behavioral data.

Although we were mainly interested in neural correlates of emotion processing, behavioral data can serve as an indicator that conflict monitoring is indeed involved in our task. A robust indicator for cognitive control induced by conflict monitoring is the behavioral conflict adaptation effect, which refers to the finding that the effect of response conflict on the current trial is reduced if response conflict was high on the previous trial (Botvinick et al., 2001; Gratton et al., 1992). In the present task, the three stimulus categories are associated with different levels of response conflict: While response conflict is highest in incongruent stimuli, it is lower in neutral and congruent stimuli. Accordingly, we expected that performance differences between these three stimulus categories - reflecting response conflict on the current trial - should be small following incongruent trials (= high response conflict on the previous trial) but larger following congruent and neutral trials (= low response conflict on the previous trial).

For computing mean response times (RTs), we excluded trials with RTs less than or greater than four standard deviations below or above the mean, determined separately for each condition and participant. Less than 1% of trials were excluded. Mean RTs and error rates for each combination of stimulus categories in the current trial and the previous trial are shown in Figure 2. Whereas error rates were consistently low in all conditions, we obtained a clear conflict adaptation effect in the RTs. RTs were strongly increased for incongruent stimuli as compared to congruent and neutral stimuli following neutral and congruent trials. In contrast, such an effect was absent following incongruent trials.

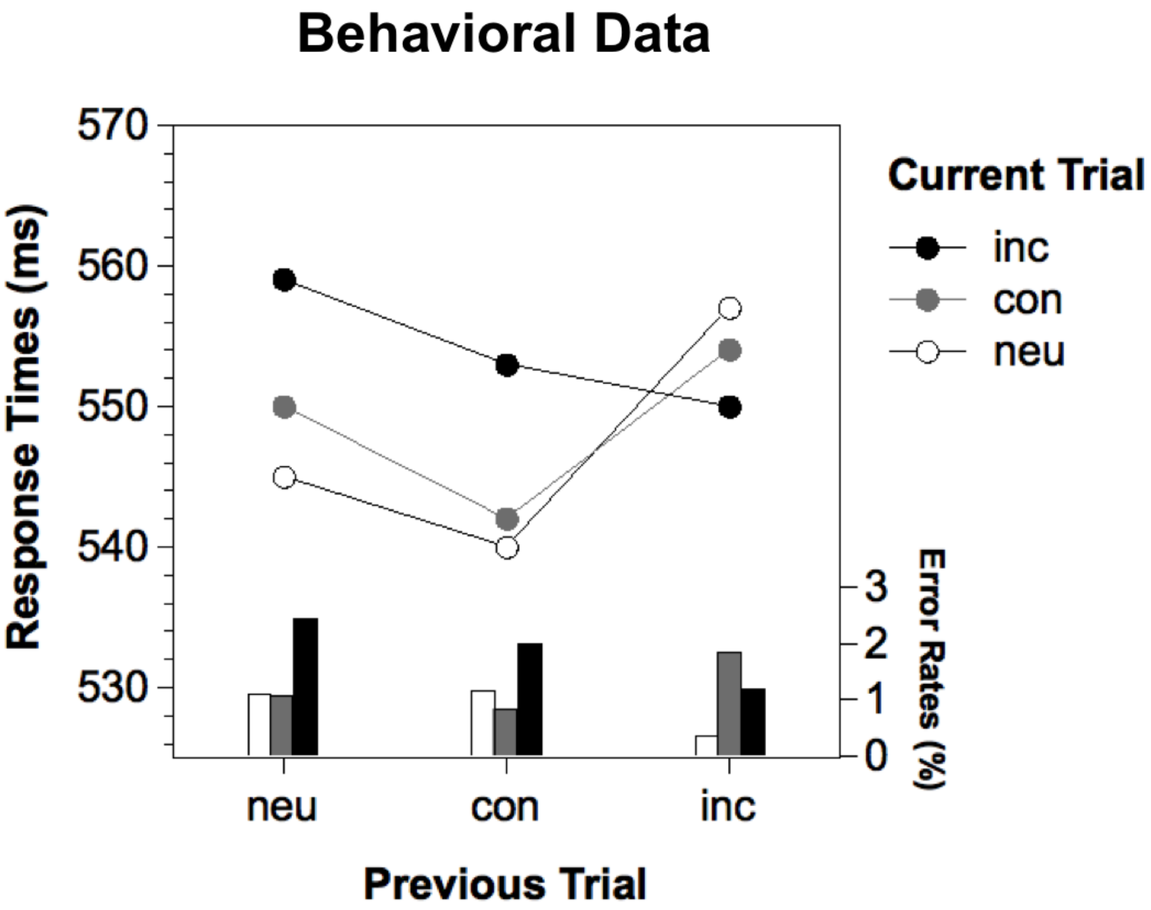

Figure 2: Response times (lines) and error rates (bars) from each combination of stimulus category on the current trial and stimulus category on the previous trial. neu = neutral, con = congruent, inc = incongruent, ms = milliseconds.

This conclusion received support from statistical analysis. A 3 x 3 ANOVA including all nine conditions revealed a significant interaction between Previous Trial and Current Trial, $F(4, 52) = 2.61$, $p < .05$. Because the conflict adaptation hypothesis refers to levels of response conflict and not to stimulus categories per se, we conducted a second analysis in which stimuli with high response conflict (i.e., incongruent) were contrasted with stimuli with low response conflict (i.e., neutral, congruent) in the current or previous trial. The respective 2 x 2 ANOVA with the variables previous response conflict (low, high) and current response conflict (low, high) also revealed no significant main effects but a significant interaction, $F(1, 13) = 11.68$, $p < .005$. Post-hoc tests confirmed that current response conflict was significant if previous response conflict was low, $p < .02$, while no such effect was obtained if previous response conflict was high, $p = .41$. The same analyses conducted for the error rates revealed no significant effects.

Conflict adaptation effects can potentially reflect stimulus priming (Mayr, Awh, & Laurey, 2003) because stimulus repetitions (or stimulus category repetitions) can occur only in those sequences in which response time benefits would mimic a conflict adaptation effect (i.e., congruent-congruent and incongruent-incongruent). However, such an explanation cannot be applied to our study because neutral-congruent sequences and congruent-neutral sequences showed similar results than congruent-congruent sequences. Nevertheless, we also conducted all analyses with the additional variable Response Transition (repetition, switch), because stimulus repetitions are restricted to response repetition trials. This variable did not interact significantly with any of the effects of interest (all *F*s < 1) which precludes that our effects are due to stimulus priming.

3.2 Effects of cognitive control on preferential sensory processing of affective stimuli.

The behavioral data suggest that the influence of the face distractor on behavior is reduced when the previous trial was associated with high response conflict. In non-emotional tasks, results like this have typically been attributed to changes in selective attention (Botvinick et al., 2001; Egner & Hirsch, 2005). In the present study, we examined whether the same effect in an emotional task is achieved by attenuating preferential processing of the affective face distractor. Preferential processing of affective distractors was measured by contrasting activity in trials with affective distractors (incongruent, congruent) with activity in trials with non-affective distractors (neutral). To ensure that this measure is not confounded with response conflict, we also compared congruent with incongruent trials on the current trial. We then tested the hypothesis that preferential processing of affective distractors is smaller following trials with high response conflict (incongruent) than following trials with small response conflict (neutral, congruent).

Our analyses focused on activity from three areas along the ventral stream of visual processing: Striate areas (BA 17), category-unspecific extrastriate areas (BA 18/19), and the face-specific FFA. Figures 3ADG show the location of these individual ROIs as an overlay plot. The color of each voxel indicates for how many participants this voxel contributes to the ROI. Figures 3BEH show the mean activity in these ROIs during the main task, computed separately for each combination of the stimulus category on the current trial (neutral, congruent, incongruent) and the stimulus category on the previous trial (neutral, congruent, incongruent). Figures 3CFI show the same data collapsed across congruent and incongruent stimuli in the current trial. These latter figures highlight our effects of interest, the modulation of preferential processing (emotional vs. neutral) as a function of previous conflict.

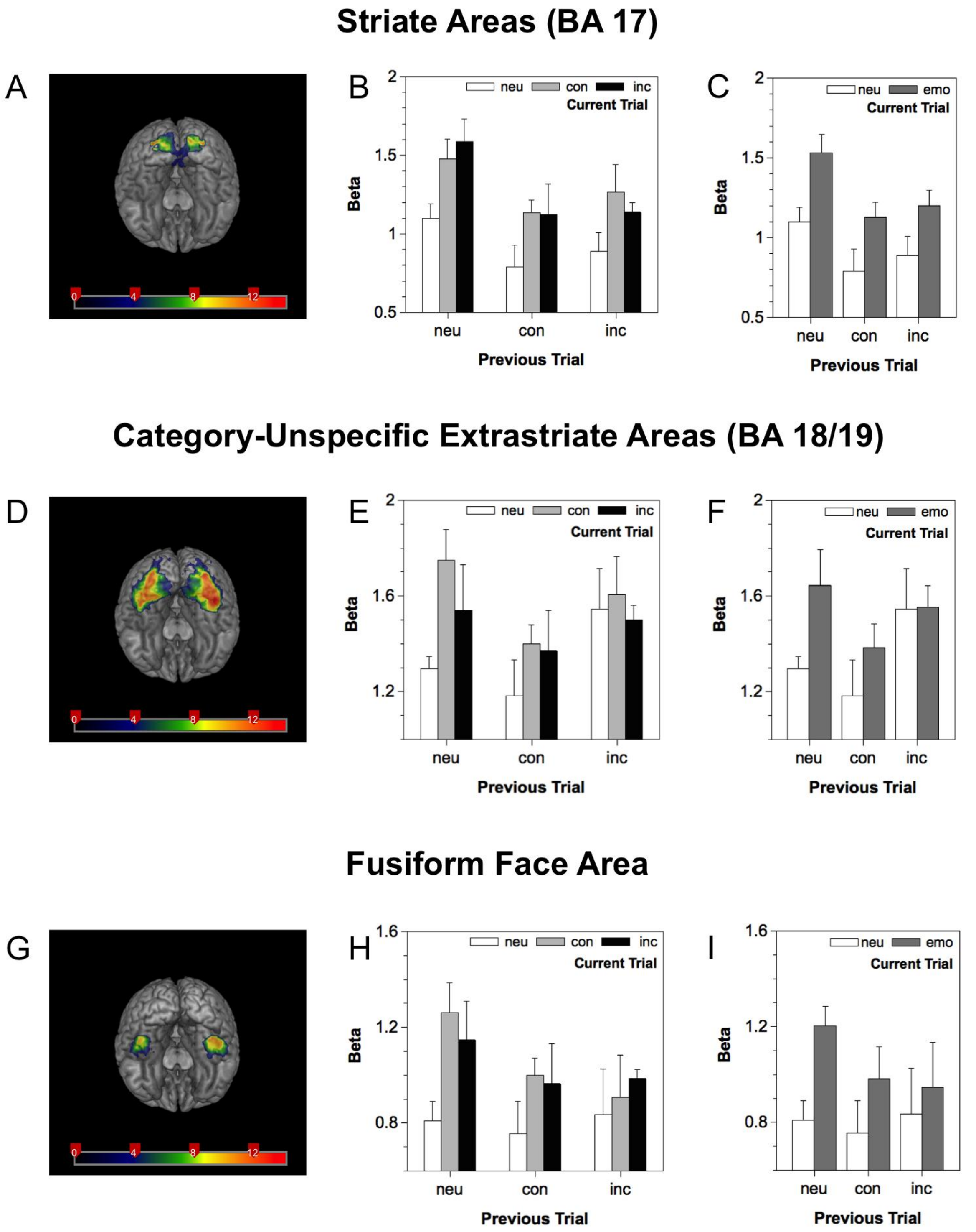

Figure 3: Regions-of-interest (ROIs) and mean activity during the main task in striate areas (A, B, C), category-unspecific extrastriate areas (D, E, F) and the fusiform face area (G, H, I). A, D, G: Location and size of individual ROIs. The color bar indicates the number of ROIs associated with each voxel. B, E, H: Mean activity in ROIs from each combination of stimulus category on the current trial and stimulus category on the previous trial. C, F, I: Mean activity collapsed across congruent and incongruent stimuli in the current trial. Overlaid ROIs are shown from a posterior-basal view. neu = neutral, con = congruent, inc = incongruent, emo = emotional.

To test our hypothesis, we applied the following analytical strategy to data from each area: We started with a 3 x 3 ANOVA including all conditions to test for overall effects of stimulus categories on the current and the previous trial. We then tested whether it is valid to merge congruent and incongruent stimuli in the current trial by conducting a 3 x 2 ANOVA with the variables Previous Trial (neutral, congruent, incongruent) and Current Trial (congruent, incongruent). If this analysis revealed no significant effects involving Current Trial, we conducted a final 3 x 2 ANOVA with the variables Previous Trial (neutral, congruent, incongruent) and Current Trial (affective, non-affective). In this analysis, the variable Current Trial directly represents the strength of preferential processing of affective (i.e., congruent and incongruent) face distractors relative to non-affective (i.e., neutral) face distractors.

Striate Area (BA 17). The data in Figure 3BC reveal a strong effect of preferential processing of affective face distractors. Activity is larger for stimuli containing affective faces than for stimuli containing non-affective faces. However, this effect appears to be independent of the stimulus on the previous trial. This conclusion receives support from statistical analyses. The 3 x 3 ANOVA including all conditions revealed a significant effect of Current Trial, $F(2, 26) = 5.69$, $p < .009$, and a marginally significant effect of Previous Trial, $F(2, 26) = 2.88$, $p < .08$, but no significant interaction, $F(4, 52) = .62$, $p = .65$. Because no significant effects involving Current Trial were obtained when only congruent and incongruent trials were included (Fs < .75), we conducted a 3 x 2 ANOVA including the variable Current Trial (affective, non-affective). We again obtained a significant effect of Current Trial, $F(1, 13) = 19.8$, $p < .001$, and a marginally significant effect of Previous Trial, $F(2, 26) = 2.60$, $p < .10$, but no significant interaction, $F(2, 26) = .43$, $p = .65$. These results suggest that while there is preferential processing of affective face distractors in striate areas, this effect is not influenced by cognitive control.

Extrastriate Areas (BA 18/19). The data in Figure 3EF suggest that, in contrast to striate areas, preferential processing of affective distractors in extrastriate areas is obtained only following neutral and congruent trials while it is absent following incongruent trials. Indeed, the 3 x 3 ANOVA revealed a significant interaction between Current Trial and Previous Trial, $F(4, 52) = 2.92$, $p < .03$. Main effects of Current Trial, $F(2, 26) = 1.32$, $p = .29$, and Previous Trial, $F(2, 26) = 1.14$, $p = .34$, were not significant. Crucially, this interaction can be ascribed to differences between affective and non-affective distractors. Whereas no differences between congruent and incongruent trials (all $F < .71$) were obtained, the final 3 x 2 ANOVA including Current Trial (affective, non-affective) also found no significant main effects of Current Trial, $F(2, 26) = 1.78$, $p = .21$, and Previous Trial, $F(2, 26) = 1.33$, $p < .29$, but a significant interaction, $F(2, 26) = 8.10$, $p < .002$. Post-hoc tests revealed that the difference between affective and non-affective distractors was significant following neutral ($p < .001$) and congruent trials ($p < .02$) but not significant following incongruent trials ($p = .99$). These results clearly demonstrate a reduction of preferential processing of affective distractors in extrastriate areas when the previous trial was associated with high response conflict.

Fusiform Face Area (FFA). Figure 3HI shows a similar pattern for the FFA as for the category-unspecific extrastriate areas, although the effect sizes were clearly weaker. In the 3 x 3 ANOVA, no significant main effects of Current Trial, $F(2, 26) = 2.14$, $p = .14$, and Previous Trial, $F(2, 26) = .55$, $p = .58$, were obtained. However, the interaction only scarcely failed to reach significance, $F(4, 52) = 2.52$, $p = .053$. While the ANOVA including only congruent and incongruent trials revealed no significant effects (all Fs < 1.38), the ANOVA comparing affective and non-affective distractors revealed a significant interaction, $F(2, 26) = 3.51$, $p < .05$. Post-hoc tests showed that the difference between affective and non-affective distractors was significant following neutral ($p < .001$) and congruent trials ($p < .05$) but not significant following incongruent trials (p = .71). As for the category-unspecific areas, these results show a reduction of preferential processing of affective distractors following high response conflict.

Joint Analyses of Striate Areas, Extrastriate Areas and FFA. To statistically corroborate that the patterns indeed differ across ROIs, we analyzed the data in a single analysis including the variables Previous Trial, Current Trial and ROI. The crucial three-way interaction was marginally significant, $F(8, 104) = 1.77$, $p = .09$, which might reflect that our design has not enough power for this higher-order interaction. As we had no differential hypothesis for congruent and neutral stimuli on the previous trial, we collapsed across these two categories and recomputed the ANOVA. In this reduced design, the respective interaction reached significance, $F(4, 52) = 3.07$, $p < .03$. This effect was predominantly caused by differences between V1 and the other two ROIs. The same ANOVA computed for pairwise ROIs revealed significant or marginally significant three-way interactions when FFA and V1, $F(2, 26) = 3.99$, $p < .04$, or extrastriate areas and V1, $F(2, 26) = 2.84$, $p < .08$, were compared, but no significant effect when extrastriate areas and FFA, $F(2, 26) = 1.58$, $p = .23$, were compared.

Control Analyses. In addition, we conducted several control analyses. We reanalyzed the data including the additional variable Response Transition (response repetition, response switch) in all analyses to investigate again whether our results are related to stimulus or response priming (Mayr et al., 2003). However, this variable did not interact with any of the crucial interactions between previous and current stimulus category. In further analyses, we investigated whether our effects differ according to emotional valence (happy, fearful) of the current trial. This was not the case, irrespective of whether the analyses involved the variables Target Valence or Distractor Valence (while excluding conditions with neutral distractors).

PPI-Analysis (BA 18/19 & FFA combined). The PPI analysis of the higher-order visual seed regions revealed one supra-threshold cluster in the region of the right orbitofrontal cortex, covering posterior, medial and lateral orbital regions (k = 231, p = .012, FWE-corrected at cluster level; MNI [27, 24, -15], [18, 30, -18], [36, 30, -24], [39, 42, -15], [18, 36, 0]; Fig 4A). In addition, in accordance with a priori assumptions a further cluster was revealed in the left rACC, which did not surpass whole head corrected statistical criteria (Fig. 4B). However, applying small volume correction around coordinates previously reported to be involved in emotional conflict regulation confirmed that the rACC indeed was functionally coupled to higher-order visual processing regions during the regulation of preferential emotion processing (k = 132, p = .009, FWE-corrected at cluster level; MNI [0, 57, -15], [-12, 36, 18], [-12, 45, 9]).

In sum, our analyses demonstrated preferential processing of affective distractors in striate and category-unspecific extrastriate areas and the FFA. Most importantly, we found that for extrastriate areas and the FFA, this effect was modulated by cognitive control. Following trials with high response conflict, preferential processing of affective distractors in these areas was virtually abolished. Moreover, this effect was mediated by the rACC, a region that has previously been shown to be involved in control of emotion-mediated conflict.

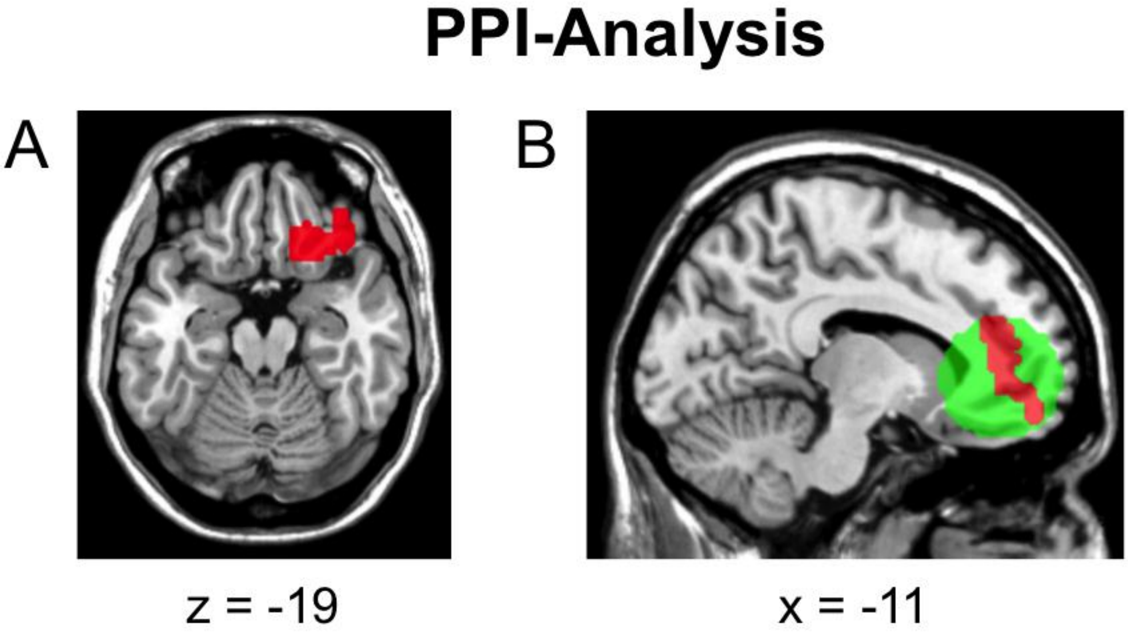

Figure 4: Brain regions showing increased functional coupling with higher-order visual cortex during preferential emotion processing after incongruent as compared to congruent preceding trials. A) Significantly coupled cluster in right hemispheric orbitofrontal cortex. B) Significant results in the rostral anterior cingulate cortex (rACC) replicate previous research and confirm the rACC‘s presumed role in the regulation of emotional conflict. Green areas indicate the volume utilized for small volume correction.

4. Discussion

Preferential sensory processing of affective stimuli has often been viewed as a merely automatic process that is largely unaffected by cognitive control (for a discussion, see Vuilleumier, 2005). In the present study, we tested the validity of this notion by examining whether preferential processing of an affective but irrelevant face stimulus is suppressed when a face distractor has caused a conflict on the previous trial. Using a strictly theory-driven approach, our specific hypotheses were derived from the integration of two theoretical frameworks: Based on studies from the emotion literature (Morris et al., 1998; Pessoa et al., 2002; Vuilleumier et al., 2001), we constructed a measure of preferential processing of affective face distractors and derived predictions in which regions of the stream of visual processing such an effect should be obtained (the striate area, category-unspecific extrastriate areas, and the FFA). Based on studies on cognitive control and conflict monitoring (Botvinick et al., 2001), we derived the prediction that cognitive control should be increased following trials with high response conflict relative to trials with low response conflict, and that this should be mirrored by a reduction of preferential processing of affective face distractors.

Our data revealed a modulation of preferential processing by cognitive control in category-unspecific extrastriate areas and the FFA. Following trials with low response conflict, we found increased activity for affective face distractors relative to non-affective face distractors in voxels that previously responded to face stimuli in a localizer task in these regions. Following high conflict trials, however, this preferential processing of affective distractors was not only reduced but even eliminated. This suggests that, upon detection of an emotion-mediated response conflict, a conflict monitoring system initiates control processes which suppress the ability of affective stimuli to be preferentially processed in sensory areas. Our data suggest that the earliest time point at which this suppression occurs is processing in extrastriate areas of the ventral stream. Although we obtained substantial preferential processing of affective faces also in striate areas, this was independent of previous response conflict, and hence, unaffected by cognitive control. Importantly, the analysis of behavioral correlates of response conflict further demonstrated that reduced preferential processing in extrastriate areas effectively reduced response conflicts elicited by affective distractor faces, as performance data indicate a strong conflict adaptation effect.

Please note that, in the present experimental design, preferential processing is measured by comparing affective face distractors with neutral face distractors. Because affective face distractors comprise congruent as well as incongruent stimuli, one could speculate that effects of distractor emotionality are largely driven by distractor incongruency, and hence, response conflict. However, inspection of Figure 3 demonstrates that this is not the case. In all ROIs, data for incongruent and congruent face distractors are virtually identical. That is, there is preferential processing of emotional faces relative to neutral faces irrespective of whether these faces are associated with the same or a different response as the target. These data suggest that the effects of distractor emotionality are not due to distractor incongruency, and hence, reflect preferential processing of emotional distractor stimuli.

Our findings provide support for a crucial finding of Etkin et al. (2006) and Egner et al. (2008) by showing that suppression of preferential processing of affective face distractors is mediated by changes in functional connectivity between higher-order visual areas and the rACC. This again demonstrates that the rACC is involved in cognitive control of emotion-mediated conflict. A crucial difference between their work and ours is that the consequence of conflict control in our study is a reduction of preferential processing whereas these authors demonstrated a reduced amygdala activity following conflict. We cannot definitely say whether these two findings are related. We did not find effects in the amygdala which might simply reflect that our task (responding to words while ignoring faces) and our design (with incongruent stimuli on only 1/3 of trials) induces lower levels of emotional conflict. However, it is possible that reduced preferential processing and modulation of amygdala activity reflect two faces of the same mechanism. In this respect, our study can be viewed as an extension of the work of Etkin et al. (2006) and Egner et al. (2008) and a specification of their proposed mechanism.

An important question concerns the nature of conflict that leads to the recruitment of cognitive control in the present paradigm. The original conflict monitoring account assumes that control is adjusted based on the monitoring of response conflict, that is, the simultaneous activation of contradictory motor responses (Botvinick et al., 2001). Because the present study - as virtually all studies on conflict adaptation – manipulates response compatibility between target and distractor to vary conflict, it is plausible to assume that monitoring of response conflict is involved in our paradigm. However, previous studies have shown that, in other paradigms like the flanker task, conflict adaptation can also be driven by forms of perceptual conflict (Soutschek, Taylor, Müller, & Schubert, 2013; Verbruggen, Notebaert, Liefooghe, & Vandierendonck, 2006). Furthermore, Egner et al. (2008) found an involvement of rACC in conflict resolution only in a task in which response conflict was mediated by emotional categories (as in the present study) but not when merely non-emotional categories were used. Given that we also found an involvement of the rACC in conflict resolution, it is likely that conflict in the present paradigm occurs already on the level of emotional categories, and that this aspect is critical for the emergence of our results.

Whereas our study focused on the effects of cognitive control on distractor processing, previous studies have shown that response conflict is also associated with subsequent enhanced target processing (Egner & Hirsch, 2005). In the present study, because target and distractors were spatially overlapping visual stimuli, we cannot disentangle target-related activity and distractor-related activity in category-unspecific visual processing areas. However, one aspect of our data suggests that target processing has indeed changed following response conflict. It appears that the reduced effect of distractor emotionality following response conflict in extrastriate areas is caused by an increased activity for trials with neutral distractors rather than a reduced activity for trials with emotional distractors. This might reflect the combined effect of a) reduced preferential processing of emotional distractors, and b) generally enhanced target processing following conflict in category-unspecific extrastriate activity. Such an assumption receives support from the observation that a comparable effect is not obtained in the FFA. However, one has to be cautious with this conclusion because the joint analysis did not reveal a statistically significant difference between both regions. Moreover, the data still allow for the possibility that the reduction of preferential processing in category-unspecific extrastriate regions is caused by a mechanism other than a suppression of affective distractor processing.

Our findings demonstrate that even highly automatic processes like emotional evaluation are affected by cognitive control. This is plausible given that preferential processing of affective stimuli is sometimes disadvantageous. While it normally facilitates the immediate preparation of an adequate (e.g., flight) response to a significant (e.g., threatening) sensory event, it can also impair adaptive behavior when the prepared response contradicts current goals and intentions. Under these conditions, it is advantageous that control processes should be able to turn off these mechanisms at least temporarily. This ability to actively suppress preferential processing of affective stimuli is even more important given its resistance to habituation (Schupp et al., 2006). However, our results also show that the detection of response conflict implies only a temporary reduction of preferential processing. It recovers as soon as the face distractor facilitates rather than impairs processing, as demonstrated by substantial preferential processing following trials with low response conflict. This illustrates the flexibility and adaptivity by which emotional processing can be modulated by cognitive control.

Taken together, the present results show that cognitive control can modulate preferential processing of affective stimuli under conditions where processing of affective stimuli is detrimental. We provided evidence for the notion that emotion-mediated conflicts are resolved by reducing preferential processing of affective stimuli in extrastriate sensory areas - a process that has frequently been viewed as being largely automatic and involuntary (Vuilleumier, 2005). In addition, our results provide further support for the idea that conflict monitoring is crucial for the brain to determine the need for cognitive control (Botvinick et al., 2001). Further research is required to investigate whether similar adjustments of emotional processing take place when cognitive control is recruited by response conflict associated with errors (Yeung, Botvinick, & Cohen, 2004), or by the conscious detection of errors (Maier, Steinhauser, & Hübner, 2008; Steinhauser & Yeung, 2010). Moreover, direct modulation of control using non-invasive brain stimulation during fMRI (Meinzer et al., 2014) could shed further light on the relationship between cognitive control and emotional processing.

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MS and TF contributed equally to this article. The authors declare no conflict of interest. Correspondence concerning this article should be addressed to Marco Steinhauser, Catholic University of Eichstätt-Ingolstadt, Department of Psychology, Ostenstraße 25, D-85072 Eichstätt, Germany. E-mail: Marco.Steinhauser@ku.de, or to Tobias Flaisch, University of Konstanz, Department of Psychology, Fach 36, D-78457 Konstanz, Germany. E-mail: Tobias.Flaisch@uni-konstanz.de.

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Highlights

- Affective distractor faces are preferentially processed visual areas.
- This effect is abolished in extrastriate areas when distractors previously caused conflict.
- Preferential sensory processing of affective stimuli is influenced by cognitive control.
- Control is mediated by functional coupling between extrastriate areas and rACC.